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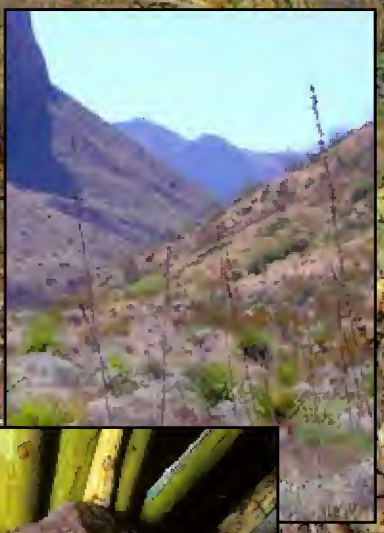
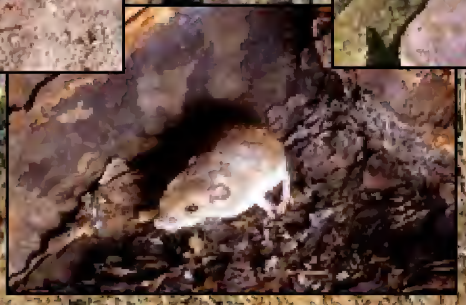
Movements, Populations, and Habitat Preferences of Three Species of Pocket Mice (Perognathinae) in the Big Bend Region of Texas





Richard D. Porter
Calvin A. Porter, Editor

Front cover: Background photograph is the Merriami plot at Panther Junction, looking southwest towards the Chisos Mountains (May 2011). Lower center inset: *Perognathus merriami*. Left insets: *Chaetodipus eremicus* and the Eremicus plot (May 2008) looking southwest. Right insets: *Chaetodipus nelsoni* and the Nelsoni plot (May 2008) looking northwest with Nugent Mountain on the left. The arrangement of the photographs represents the ecological distribution of the three species of pocket mice in Big Bend. *Chaetodipus eremicus* commonly occupies flat, open, rock-free sandy or loamy areas, while *C. nelsoni* is found most commonly in steep, rocky, and often densely vegetated habitats. *Perognathus merriami* can occupy a wide range of habitats, but in the presence of the larger *Chaetodipus* species is most abundant in habitats intermediate to those occupied by *C. nelsoni* and *C. eremicus*. Pocket mouse photographs were taken during the study by R. D. Porter. Habitat photographs and cover design by C. A. Porter.

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FOREWORD

Background of the Study

My father, Richard D. Porter, completed his B.S. at the University of Utah in 1950 and his M.S. in 1952. His thesis advisor was Dr. William H. Behle, and his thesis was entitled *The Hungarian Partridge in Utah, with Special Reference to Ecology and Life History* (Porter 1951, 1955). He worked for two years as an ecologist at Dugway Proving Grounds before enrolling in a Ph.D. program at the Agricultural and Mechanical College of Texas (now Texas A&M University) in 1955. His doctoral program was directed by Dr. William B. Davis.

Upon completing his course work in June 1957, my father moved with his family to Big Bend National Park (BBNP) for more than two years, during which time he conducted field work on the ecology of pocket mice (Plate 1). He compiled more than 18,000 trap nights and carefully recorded data about vegetation, soil, habitats, movements, reproductive condition, parasites, pelage, and other life history characteristics. This ambitious effort was just a portion of the study originally envisioned. The original research prospectus also included proposed studies of systematics, diet, and burrow architecture. "As the study progressed," he wrote, "the scope of the investigation was reduced commensurate with the time available." The result of this "reduced" two-year field study was a 255-page dissertation (Porter 1962) which is published here (in edited form) for the first time. The study was funded by the Texas Game and Fish Commission under contract with the Texas Agricultural Experiment Station. In addition to pocket mice and other mammals, my father collected birds, reptiles, amphibians, and parasitic arthropods (Wiseman 1959; Eads 1960; Degenhardt 1966; Wauer 1969, 1973a, c; Fleet and Dixon 1971), and conducted population surveys of deer, all as part of the larger project that funded the research. Specimens collected during the study are now deposited in collections at BBNP, Texas A&M University, Brigham Young University, the Smithsonian Institution, and elsewhere. During the study, he collected two previously undescribed species of fleas (Eads 1960), three species of undescribed mites (discussed in this study), and four undescribed species of avian chewing lice (Wiseman 1959).

Plate 1. The author, Richard D. Porter, in Big Bend National Park, ca. January 1959. Photographer unknown.

An accomplished photographer, my father took hundreds of photographs of the habitat, flora, and fauna of BBNP. Many of his photographs were included in the second edition of *The Mammals of Texas* (Davis 1960) and some still appear in the current sixth edition (Schmidly 2004). Other Big Bend photographs were published in *Naturalist's Big Bend* (Wauer 1973b, 1980; Wauer and Fleming 2002) and *Birds of Utah* (Hayward et al. 1976). Several were displayed for many years at Park Headquarters.

While conducting field work, he resided with his family in a trailer at Panther Junction. My mother, Lois Gunderson Porter, was hired as the Park's schoolteacher (Tucker 2008), and taught grades 1-8 in a single classroom in the small San Vicente School at Panther Junction. For much of her tenure, she was the only teacher in the Park. My father was employed for $25 per month as the school custodian. My mother frequently assisted with his research, particularly with trapping, substrate analysis, and recording data in the field. My brothers Sanford (now a USDA research entomologist in Gainesville, Florida) and Neil (who died at age 6 in a tragic accident in August 1961) ranged in age from 2 to 5 during the study, and often accompanied my father into the field while my mother was in the classroom. I was born in August 1959 as the field study concluded. Because the Park had no physician on staff, and my family was preparing to relocate to El Paso as my birth approached, my mother and brothers traveled to Salt Lake City where they stayed temporarily with family until I was born. My father stayed at the K-Bar Ranch in the Park for a few more weeks. He trapped the final habitat plot (plot 101) during that time, and museum records indicate he collected bats in Big Bend up to five days before my birth. That he would still be collecting mammals with his expectant wife 2,000 km away attests to his dedication to research, and perhaps was a portent of my becoming a mammalogist after him.

A few weeks later, as soon as I was old enough to travel, my family settled in El Paso, Texas, where my father taught at Texas Western College (now the University of Texas at El Paso) for the 1959-1960 academic year. We moved to Salt Lake City in June 1960, where my father spent about a year working on analysis and writing. In the fall of 1961, he took a teaching position at what was then known as Wisconsin State College—Whitewater. During his first year at Whitewater, he put the finishing touches on the dissertation, and returned to College Station in July 1962 to defend the dissertation. The degree was awarded in August 1962

After leaving Whitewater in 1965, my father taught biology at the New Mexico Institute of Mining and Technology. In 1967, he began work for the U. S. Fish and Wildlife Service, first at the Patuxent Wildlife Research Center near Laurel, Maryland, and then (beginning in 1973) for the Denver Wildlife Research Center, stationed in Provo, Utah. At Patuxent, he performed research (e.g., Porter and Wiemeyer 1969, 1972; Wiemeyer and Porter 1970) on the effects of DDT and other pesticides on American Kestrels (*Falco sparverius*). His work at Provo involved ecological surveys of raptors, particularly the Peregrine Falcon (*Falco peregrinus*) in the western United States and Baja California (e.g., Porter and White 1973, 1977; Porter et al. 1988). He retired from the Fish and Wildlife Service in 1980, and spent his retirement in Mapleton and Brigham City, Utah, and finally Gainesville, Florida. He died in Gainesville on 2 October 2007 at the age of 84.

Impact of the Study

Due to the demands of teaching and government service, my father was never able to complete preparation of the dissertation for publication. Although it has not been entirely ignored, the impact of the work has been narrowed by its unpublished status. Relatively few authors (Davis 1966, 1974; Baccus 1971; Boeer and Schmidly 1977; Schmidly 1977a, b; 2004; Davis and Schmidly 1994; Best 1994; Best and Skupski 1994; Wu et al. 1996; Yancey et al. 2006; Punzo 2007) have directly referenced the dissertation, but some of the basic findings of the study have made their way into the pocket mouse literature via citations from these secondary sources. In several cases, while working on updating the literature citations, I encountered references which seemed to provide recent supporting data, only to find upon tracing the reference to its source, that the ultimate origin of the information was the very dissertation I was updating!

The dissertation was cited a dozen or more times each in the *Mammalian Species* accounts of *Perog-*

nathus merriami and *Chaetodipus nelsoni* (Best and Skupski 1994; Best 1994). These citations include references to field methods, identification, morphology, molting, habitat, population, reproduction, life history, ectoparasites, home range, territoriality, activity, and community structure. The number and breadth of these citations in the species accounts demonstrate the importance of the study to knowledge of the biology of these species. Schmidly (1977b) referred to Porter's (1962) "excellent analysis of the influences of substrates on local distribution and abundance of three species of pocket mice."

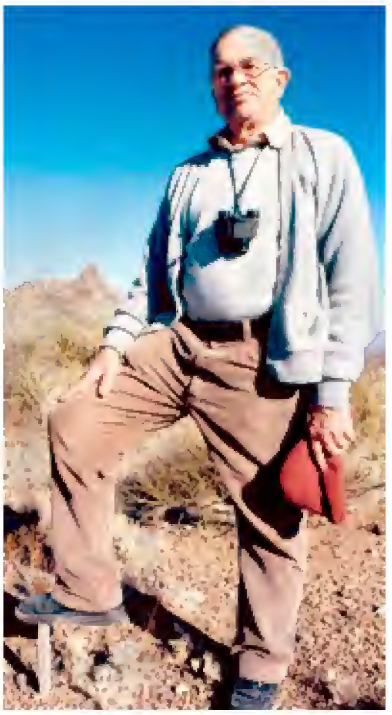

Plate 2. Richard D. Porter at the Merriami plot, 30 December 1988. Lone Mountain in the background. Photograph by C. A. Porter.

Taxonomy

My father disagreed with Wilson's (1973) action to synonymize *Perognathus merriami* with *P. flavus*. According to correspondence in his files, the issue came up as early as 1965 in conversations with Sydney Anderson at the annual meeting of the American Society of Mammalogists in Winnipeg. Later that year, Anderson sent my father excerpts from his forthcoming manuscript on the mammals of Chihuahua (Anderson 1972) showing morphological differences between *P. flavus* and *P. merriami*. Anderson agreed that the two species were distinct and concluded that "it is possible, of course, that some of the differences that seem to distinguish the two species in Chihuahua would not do so in some other part of their range, or that differences might occur in some other area that do not occur in Chihuahua. In any event, I am convinced that two distinct species are involved" (S. Anderson, pers. comm. to R. D. Porter, 3 August 1965). My father was pleased when Lee and Engstrom (1991) published molecular evidence supporting the validity of *P. merriami*.

Subsequent Activities

In December 1988 my parents and I visited the study area in BBNP and found some wooden stakes marking the trap sites (Plate 2). I visited the area again with my mother in May 2008 to qualitatively assess changes on the three population plots and map the boundaries of the plots using GPS. I returned in November 2008 and took additional photographs and finished mapping the plots. On these trips, we located at least one metal corner stake in each plot, along with numerous wooden stakes that after 50 years, still marked the trap stations. As a result, we were able to more accurately map the location and orientation of the plots.

A total of 76 habitat plots (numbered non-consecutively from 1 to 101) were assessed during the study. My father did not list the specific localities of all 76 habitat plots (Porter 1962), but stated that the full list of localities would be deposited at BBNP and the Texas A&M Department of Wildlife Management. In 2007 and 2008, I contacted personnel at BBNP and Texas A&M; they were unable to locate the locality list. I also was unable to find the list in a thorough search of my father's professional and personal files. Complete field notes were available only for the first half of the study, and the locality numbering system used in the field notes did not correspond to that used in the dissertation. Specimens collected from the habitat plots are deposited in the mammalogy collection at Brigham Young University, but plot numbers were not recorded on the tags. Localities for some of the habitat plots were

listed in the dissertation, and I was able to determine some others from notations on photographs of the plots. This information has been incorporated into the text and figure legends.

Copies of my father's field notes and other documents related to this study along with my father's ornithological notes from his work at Big Bend, are archived at BBNP. The original dissertation (Porter 1962) and additional photographs of study sites and of the flora and fauna of the study can be accessed at http://webusers.xula.edu/cporter/rdporter/.

Preparation of the Manuscript

Other than in the Foreword and Afterword, which are signed by me, the author is writing in the first person. Where I added or revised material in the text, I did so in my father's voice so as to maintain a consistent narrative mode. The following is a summary of revisions in the manuscript.

- I have incorporated modifications indicated by the author in handwritten notations on his copy of the dissertation and by revisions he made in preparing the work for publication. He made some corrections, revisions in wording, and in a few instances, added additional information.

- Following recommendations of the referees, I have shortened and omitted some sections that are redundant or of lesser importance. I summarized the results of preliminary studies and abridged some sections, instead citing the original dissertation for more detailed analyses and discussion. The sequence of some sections has been rearranged. I have omitted some tables and figures, combined some figures, and converted the data in some tables into graphs. I added locality information for some habitat plots.

- I converted all measurements to metric units. In some cases, I made a judgment call on the precision of the measurement, and rounded the metric equivalent accordingly. Trailing zeros to the left of the decimal point should not be considered significant unless the value is used in association with other measurements indicating greater precision.

- Nearly all figures have been redrawn, and in some cases redesigned to more clearly depict the data. The maps of the population plots were redrawn and corrected based on field work in 2008. Where needed, I converted the scale of graphs to metric units. The photographic plates of Porter (1962) were cropped contact prints of 4x5 monochrome negatives exposed with a Graflex Super D camera. Although the original negatives are in my possession, I substituted 35 mm Kodachrome transparencies taken by my father at the same time and from the same vantage points. I also included some of my own photographs.

- The nomenclature of organisms has been revised to reflect current taxonomy. I added several paragraphs on heteromyid systematics and taxonomy, to describe changes that occurred since the study was carried out. Because two species have been moved out of the genus *Perognathus*, I made the appropriate revision in the title, and the collecting plots originally referred to as "*Perognathus* plots" are designated "population plots."

- I added a description of changes observed on the population plots in the fifty years since the original study.

- I was able to greatly expand the section on ectoparasites using information from the published literature, my father's notes and correspondence, and my communication with a number of parasitologists. The revised parasite section includes additional information regarding undescribed species which my father collected during the study, type localities, the disposition of specimens, and records of parasites collected from mammalian hosts other than pocket mice.

- I have added more than 60 recent literature citations pertinent to the work, but I have not

made an effort to comprehensively update all citations. The original citations to literature of the 1950's and earlier remain in the text. Although recent references might be used in place of many of the original citations, I felt that a complete modernization of the literature citations would unnecessarily distance the work from the context in which it was performed and written.

- I made changes in format to conform to modern conventions and the style of the *Special Publications*. The original dissertation did not include an abstract, so I used a modified form of the abstract published by Porter (1963). I also corrected typographical and other errors, and where appropriate, revised the wording to be more clear and concise.

Acknowledgments

Although my contribution might be sufficient to justify co-authorship, I have chosen not to dilute credit for my father's work. A case could also be made for adding my mother to the author line for her effort in the field. However, the majority of recognition for this work belongs to my father for his two years of intensive field work and two years of analysis and writing. My understanding of my father's effort increased immensely when I visited the Nelsoni plot, located on a steep grade more than 85% covered knee-deep in plants, nearly all of them spiny. While nursing bloody lechuguilla wounds in my shins, I began to appreciate the work involved in setting up a grid of 784 trap sites, then routinely traversing this difficult terrain while moving, setting, and checking traps, surveying vegetation, and sampling rocks and soil during the trapping period of more than a year. On some occasions when the dirt road was impassable, he hiked more than a kilometer on foot to reach the plot. The work on the Nelsoni plot was just a fraction of the effort involved in this study, for which due credit should be given the author.

Numerous people assisted with preparing the manuscript for publication. Lois G. Porter, an invaluable participant in the original field research, provided field notes, catalogs, correspondence, and many other documents related to the study. She provided extensive information, answered many questions, helped to identify collecting sites, and provided funds to cover field work and publication costs. Field work in 2008 was authorized by the National Park Service (Permit BIBE-2008-SCI-0025). Raymond Skiles authorized the work and Susan Simmons assisted with accommodations at the K-Bar Ranch. Lois G. Porter and Mark A. Porter assisted in the field.

Christine L. Hice, Thomas E. Lee, Sanford D. Porter, and David J. Schmidly reviewed the manuscript and provided valuable suggestions. Lisa C. Bradley provided helpful editorial assistance. John O. Whitaker, Jr. and Brianne Walters of Indiana State University and D. A. Crossley, Jr. of the University of Georgia provided information and advice regarding the ectoparasites collected during the study. Ann M. Porter provided advice and assistance in preparing figures and in revising the text. The following people assisted with locating documents, specimens, and other information: Jeffery Bennett and Sue Buchel (BBNP); Debra Creel and Ronald Ochoa (USDA Systematic Entomology Laboratory); James R. Dixon, Thomas A. Lacher, Jr., and Heather Prestridge (Texas A&M University); Bruce D. Eshelman (Wisconsin State University, Whitewater); Jerry Louton (National Museum of Natural History), Barry M. OConnor and Priscilla Tucker (University of Michigan); Steven Platt (Sul Ross State University); Eric Rickart (University of Utah); Duke S. Rogers (Brigham Young University); Cal Welbourn (Florida Department of Agriculture & Consumer Services); and Franklin D. Yancey, II (State Center Community College).

I thank all of these people in addition to those mentioned in the author's Acknowledgments.

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ABSTRACT

Population characteristics and habitat preferences of Merriam's pocket mouse (*Perognathus merriami),* Nelson's pocket mouse (*Chaetodipus nelsoni)*, and the Chihuahuan pocket mouse (*C. eremicus*) in the Big Bend region of Texas were studied intensively over 26 months. Steep slopes limited the distribution and abundance of Chihuahuan pocket mice but not the other two species. Merriam's pocket mice normally were not present on steep slopes because of the usual occurrence of tall, dense vegetation on these sites, but they did occur there when the understory vegetation was sparse and short and there were either large boulders or fine gravels. Nelson's pocket mice were most abundant on slopes >20%, *P. merriami* on slopes 3-10%, and *C. eremicus* on slopes <2%. *C. eremicus* was most abundant on deep, rock-free (<5% gravel) sands, loams, and sandy loams, and was rarely found on shallow, rocky, sandy, and sandy clay loam soils. *P. merriami* was common on deep sandy loams and sandy clay loams covered with erosion pavement (rocks usually <7.5 cm in diameter accumulated on the surface) and usually containing 40-60% gravel. Nelson's pocket mouse was most abundant on shallow sandy loam or sandy clay loam soils of the mountain slopes containing cobbles and boulders (70% rocks at least 7.5 cm in diameter and frequently much larger). It was rarely found on rock-free, deep loams or sandy loams. The three species segregated themselves in the habitat according to the number and size of the rocks and the density and height of the understory vegetation. The three species of pocket mice were not restricted to specific plant associations, although each species had preferences. Nine habitat types were identified in the Big Bend area, with *C. nelsoni* commonly found in rocky, often steep and densely vegetated habitats, and *C. eremicus* in flat, rock-free, sparsely vegetated habitats. Merriam's pocket mouse, which has a wide range of habitat tolerance throughout its geographic range, reached its peak of abundance in habitats intermediate to and not preferred by the two species of *Chaetodipus*. It is believed that despite its greater range of habitat tolerance, *P. merriami* is better adapted to these intermediate habitats, and that because of its smaller size, it further tends to be crowded into this habitat by population pressures from *Chaetodipus*. During colder years, males of *P. merriami* and *C. eremicus* emerged from hibernation earlier in the spring than females. These two species showed a much stronger tendency to hibernate than did *C. nelsoni*, which was generally active throughout the winter. Reproductive activities of *C. nelsoni* started earlier in 1959 than those of the other two species, probably due to a lesser tendency of *C. nelsoni* to hibernate. The principal period of reproduction for pocket mice was in spring with a smaller fall peak. Juvenile female *P. merriami* molted into adult pelage before pregnancy occurred; juvenile females of the other two species appeared more sexually precocious. The incidence of pregnant juveniles of *C. eremicus* was higher than that of the other two species. Based on sperm production, juvenile males of *P. merriami* were more precocious sexually than juvenile males of *Chaetodipus*. Although the general progression of molt among the three species was similar, details were different. In general, adults moved greater distances than juveniles (except in September). *P. merriami* moved significantly shorter distances between captures than the other species. Analysis of the shift in center of activity from one period of capture to the next revealed that these pocket mice are relatively sedentary animals. Adult females of all three species showed a stronger tendency toward territoriality than did adult males. Several species of arthropod ectoparasites were collected from pocket mice and associated rodents, including some species not previously described.

Key words: Big Bend, *Chaetodipus*, ectoparasites, habitat, molting, *Perognathus*, pocket mice, population dynamics, reproduction

INTRODUCTION

Three species of pocket mice were studied in the Big Bend region of Texas: Merriam's pocket mouse, *Perognathus merriami*, Nelson's pocket mouse, *Chaetodipus nelsoni*, and the Chihuahuan pocket mouse, *Chaetodipus eremicus*. These species occupy adjacent and often overlapping habitats in the Trans-Pecos region of Texas (Fig. 1). Two additional species, *C. hispidus* (Denyes 1956; Schmidly 1977a; Yancey and Jones 2000) and *C. intermedius* (Yancey and Jones 2000), are found in nearby regions of the Trans-Pecos but are not known from the study area. Field work in Big Bend National Park (BBNP) was performed almost continuously from June 1957 to August 1959. The study emphasized population dynamics, home range, and habitat preference, with special reference to substrate composition. Observations were made of body weights, molts, ectoparasites, and reproduction.

Mammalian taxonomy follows Wilson and Reeder (2005), with revisions recommended for heteromyids by Anderson et al. (2007) and for ground squirrels by Helgen et al. (2009). Herpetological nomenclature follows recommendations of Crother et al. (2000), including revisions of nomenclature of whiptail lizards by Reeder et al. (2002). Names of mites were updated with reference to Whitaker and Wilson (1974) and Whitaker et al. (1993). The botanical names and identifications in this report came from McDougall and Sperry (1951), with taxonomy as updated by Jones et al. (1997).

Topography and Vegetation of the Study Area

The Big Bend is that region where the southwestern boundary of Texas, formed by the Rio Grande, resembles a large pocket (Figs. 1-2). The rugged topography is marked by isolated rocky mountains and mesas. These mountain ranges extend up to 1,500 m above the desert floor. Elevations range from about 520 m at the Rio Grande below Boquillas Canyon to 2,387 m in the Chisos Mountains 40 km to the west (Fig. 2).

The Chisos Mountains consist of a Tertiary igneous mass intruding through Cretaceous sedimentary formations. In local areas in the Chisos and Chilicotal mountains, Burro Mesa, Grapevine Hills and elsewhere throughout the region, there are other exposed intrusions of igneous rock. Some barely reach the surface and produce a rugged and rocky terrain. Others form high cliffs with steep talus slopes of large boulders. The central area of the Park is a sunken block of igneous intrusions flanked on the east by the Sierra del Carmen and on the west by the Mesa de Anguila; both are Cretaceous sedimentary formations (Maxwell et al. 1955), which are predominately limestones. The foothills of the Chisos Mountains have steep, rocky slopes, with many igneous outcrops extending through shallow soil. The steeper slopes grade into more gentle outwashes of cobbles and coarse gravels extending from the mouths of the canyons. As the slope diminishes, fine gravelly outwashes become prevalent. On the shrub-studded desert flats and rolling lowlands, gravels become scarcer and in some areas almost non-existent. Washes and arroyos of sand and gravel, originating in the mountains, interrupt the continuity of the foothills and plains. In many locations along the Rio Grande, and adjacent to some of the larger creeks and dry washes, are broad flood plains made up of deep, rock-free, fine loamy soils. Steep foothills therefore, tend to have boulders, cobbles, and coarse gravels, which grade into finer gravels and ultimately sandy and loamy rock-free soils as the slopes diminish farther from the mountains. Rodents such as pocket mice are thus presented with a variety of substrates in which they may construct their burrows.

Scrubby vegetation decreases in density as it extends into the desert lowlands from the lower mountain peaks. Mesquite (*Prosopis glandulosa*) was predominate on the deep loamy soil of the flood plains, but further from the flood plain, where silts and clays give way to sands and fine gravelly sandy loams, creosotebush (*Larrea tridentata*) was the dominate shrub. These areas of creosotebush and particularly mesquite are usually characterized by a scant understory of grasses and herbs.

Closer to the foothills, perennial grasses and lechuguilla (*Agave lechuguilla*) become abundant and produce an understory denser than the overstory. Influenced by the nature of the parental material, the

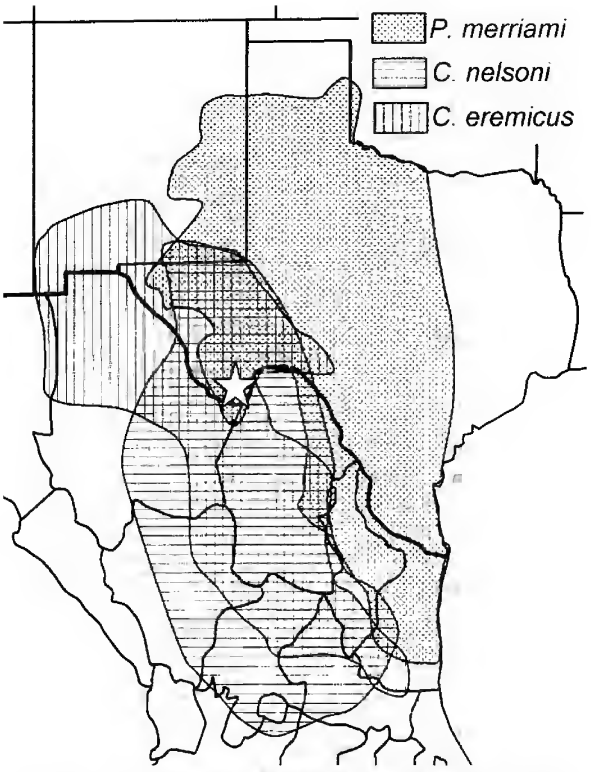

Figure 1. Geographic distribution of three species of pocket mice, modified from Best (1994), Best and Skupski (1994), and Mantooth and Best (2005b). The star indicates the Big Bend region of Texas.

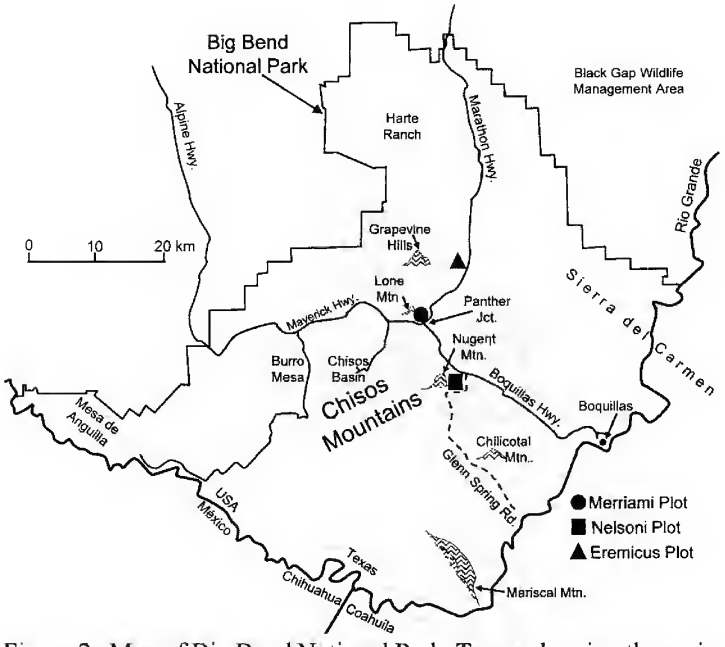

Figure 2. Map of Big Bend National Park, Texas, showing the major topographical features and the locations of the three 2.2-ha population plots. Dotted line represents an unpaved road.

soil of some fine gravelly outwashes becomes more compact in areas where the fine gravels merge with the coarse gravels and cobbles of the foothills. Under these conditions, creosotebush is gradually replaced by tarbush (*Flourensia cernua*), mariola (*Parthenium incanum*) and other, less common shrubs. Here, fluff grass (*Dasyochloa pulchella*) and lechuguilla are among the common understory plants.

In other localities creosotebush extends to the base of the foothills where it is replaced abruptly by sotol (*Dasylirion leiophyllum*), ceniza, (*Leucophyllum*), feather dalea (*Dalea formosa*), prickly pear (*Opuntia*), and other shrubs characteristic of the steeper slopes. The understory of such slopes consists principally of lechuguilla, chino grass (*Bouteloua breviseta*), and other perennial grasses. Higher in the mountains, low desert scrub gives way to woodlands of pine (*Pinus*), oak (*Quercus*), and juniper (*Juniperus*), which frequently extend down the canyons on dry creek beds in response to the greater seasonal availability of water.

Climate of the Study Area

Big Bend is in the arid zone of Thornthwaite (1948) with a moisture index of -60 to -40. The area is characterized by dry mild winters and hot summers (Figs. 3-4). During late spring and summer at lower elevations (near the Rio Grande) the mean daily maximum temperature usually is well over 38°C (Fig. 4) and frequently exceeds 43°C. In the Chisos Mountains a much cooler climate prevails. There, the mean temperature during late spring and summer generally is <32°C and seldom exceeds 38°C. Temperatures along the Rio Grande seldom drop much below freezing during the winter (Fig. 4) and snow is uncommon. However, snow falls more frequently in the mountains where sub-freezing temperatures are common. Figure 5B shows months that were above or below average monthly temperatures during the study.

Precipitation was infrequent, but often of near cloud-burst magnitude, at lower elevations. At Boquillas Ranger Station, near the Rio Grande, annual precipitation was usually less than 25 cm. In contrast, the mountainous regions usually received >25 cm annually, and 40-75 cm or more during wet years (Fig. 6). On average, rainfall in Big Bend was more frequent during spring, summer and early fall than during late fall, winter and early spring (Fig. 3).

Precipitation in the study area at Panther Junction during the investigation was above average (Fig. 6). The monthly mean precipitation was above average during the fall of 1958 and 1959 and during spring 1957 and 1959 (Fig. 5A). Precipitation was well below average in April and May 1958, August of all three years, July 1957 and during January 1959.

Systematic Relationships of Pocket Mice

Pocket mice belong to the family Heteromyidae, a clade of 59 species (Patton 2005) of burrowing, but not fossorial, rodents. Heteromyids have proven valuable as models for ecological studies of terrestrial vertebrates (Brown and Harney 1993). Three extant subfamilies and five living genera are currently recognized in the family (Anderson et al. 2007): Heteromyinae, (including the spiny pocket mice, *Heteromys*); Dipodomyinae (including the kangaroo rats, *Dipodomys,* and kangaroo mice, *Microdipodops*); and Perognathinae, (two genera of pocket mice, *Perognathus* and *Chaetodipus*). Earlier workers (Wood 1935, Hall and Kelson 1959) included *Microdipodops* in the subfamily Perognathinae, but more recent classifications (Hafner and Hafner 1983; Williams et al. 1993; Patton 2005, Anderson et al. 2007) have indicated an association between kangaroo mice and kangaroo rats in the subfamily Dipodomyinae, an arrangement first proposed by Reeder (1957).

Members of the genus *Perognathus* are usually small (100 mm) to medium (200 mm) in total length. The pelage varies from fine and silky to coarse, but never includes distinct spines or bristles. The tail may be short (about equal to body length) and tuftless, long and tuftless, or long and tufted. The soles of the hind feet are more or less hairy. Species of *Chaetodipus* are usually medium (150 mm) to large (230 mm) in size with a harsh pelage. Many of them have distinct spines or bristles that extend from the rump or sides, whereas others have no grooved spines. The soles of the hind feet are usually naked.

In the time since the study was carried out, the taxonomy of these species has been in flux. The three species studied in this investigation were regarded as

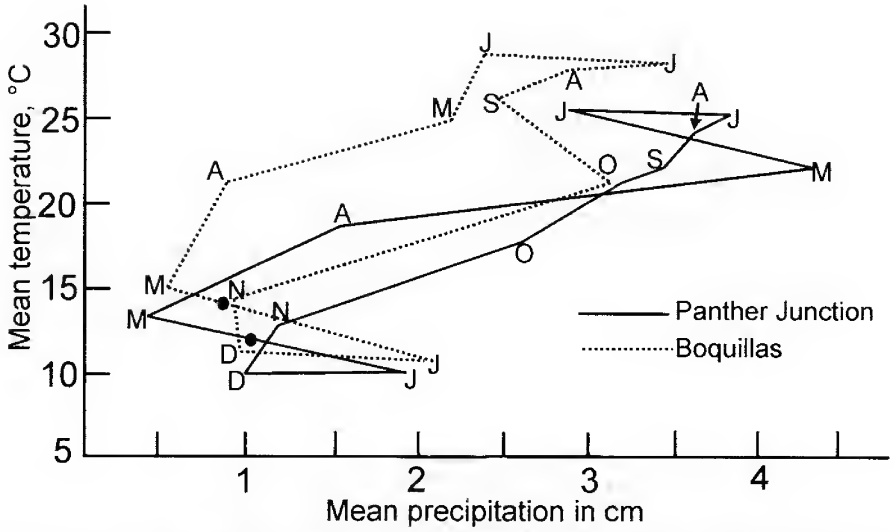

Figure 3. Hythergraphs of the average monthly mean temperature and average monthly precipitation for two weather stations in the Big Bend area. The black dots indicate the temperature and precipitation for February. Other months are represented by letters.

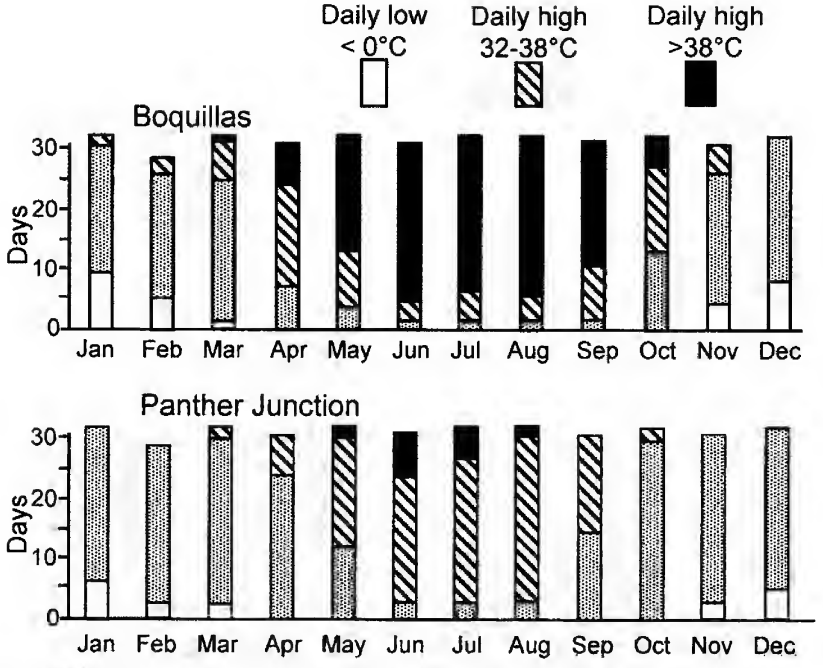

Figure 4. The average number of days during a month in which the maximum temperature exceeded 32°C or 38°C, and the number of days in which the minimum temperature fell below freezing. Gray areas of each bar indicate days in which none of these conditions occurred.

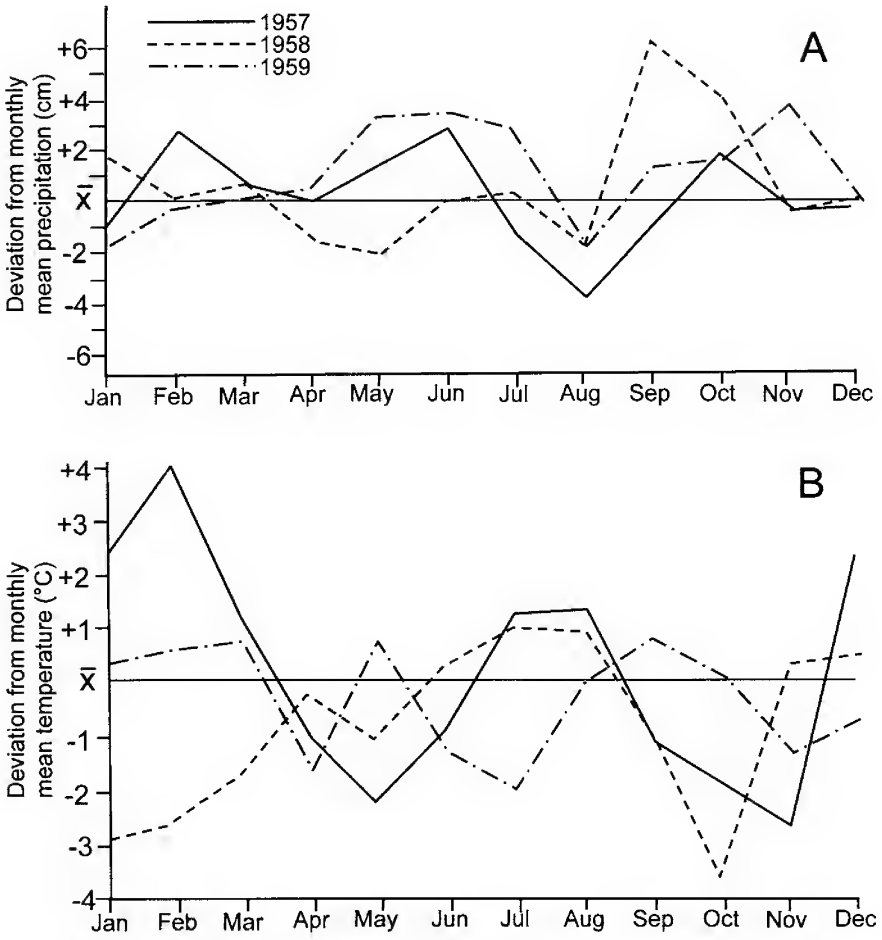

Figure 5. Monthly deviation from the mean at Panther Junction during the study period for (A) precipitation; and (B) temperature.

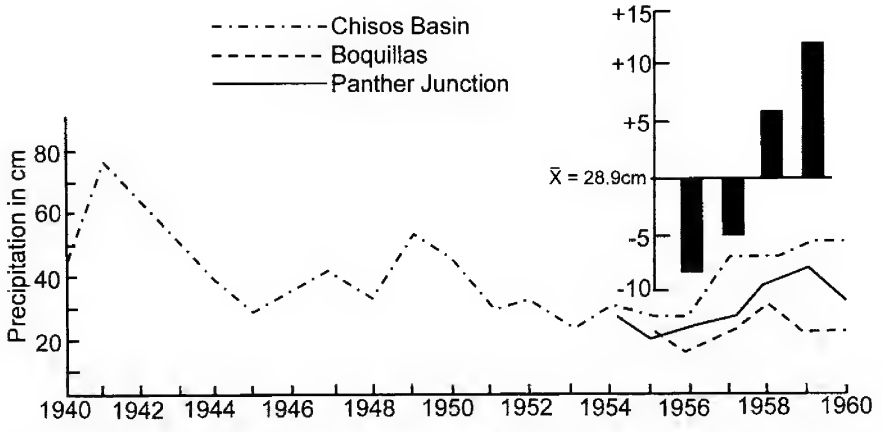

Figure 6. Annual precipitation for three weather stations in the Big Bend region of Texas. The inset bar graph indicates the annual deviation at Panther Junction during the study period from the long-term annual precipitation.

congeneric by Porter (1962), following Hall and Kelson (1959) and other authorities. The two currently-recognized genera of pocket mice were considered subgenera of the single genus *Perognathus* until Hafner and Hafner (1983) elevated the subgenera to the rank of genus, moving *P. nelsoni* and *P. penicillatus* to the genus *Chaetodipus*.

Based on morphological analysis, Wilson (1973) concluded that *P. merriami* was conspecific with *P. flavus*. This arrangement was accepted by a number of workers including Schmidly (1977a) and Hall (1981), but not by Davis (1974), who noted morphological differences between the species. Subsequently, an allozymic study by Lee and Engstrom (1991) and a DNA study by Coyner et al. (2010) showed that *P. merriami* was behaving genetically as a distinct biological species, and those authors recognized *P. merriami* as a species. Lee and Engstrom's (1991) taxonomy was accepted by Williams et al. (1993), Nowak (1999), Baker et al. (2003), Patton (2005), and Manning et al. (2008) (though not by Yancey 1997 or Yancey et al. 2006), thus reverting to the nomenclature originally used for this species by Porter (1962). Although the two species cannot be consistently identified on the basis of morphology alone, there are significant morphological differences between them (Anderson 1972; Brant and Lee 2006).

Perognathus merriami (Plate 3) is one of the smallest rodents, with an average total length of around 115 mm (Best and Skupski 1994; Schmidly 2004). It has a short tail which is usually ≤50% of the total length (Best and Skupski 1994). *P. merriami* can be distinguished from the species of *Chaetodipus* by size alone. The fine silky pelage is yellowish or ochraceous buff with white postauricular and subauricular spots (Plate 3).

The nomenclature of *C. nelsoni* has remained unchanged since Hafner and Hafner's (1983) revision, but Lee et al. (1996) divided *C. penicillatus* into two species based on mitochondrial DNA data. Findley et al. (1975) had earlier suggested that there were two species. The eastern (Chihuahuan Desert) species is now recognized by Lee et al. (1996) and subsequent authorities (Mantooth and Best 2005a, b; Baker et al. 2003; Patton 2005; Manning et al. 2008) as a distinct species, *Chaetodipus eremicus*. Patton (2005) designated this species in the vernacular to be the Chihuahuan pocket mouse.

Chaetodipus eremicus (Plate 4) and *C. nelsoni* (Plate 5) are both medium sized rodents, with *C. eremicus* an average of 153-192 mm in length (Wilkins and Schmidly 1979; Mantooth and Best 2005b, Yancey 1997), and *C. nelsoni* 156-210 mm (Wilkins and Schmidly 1979; Best 1994). Both species of *Chaetodipus* have a long tail which is well over 50% of the total length (Best 1994). The presence of white subauricular spots, well defined grooved bristles on the rump and dusky colored soles of the hind feet definitely separate *C. nelsoni* in the field from *C. eremicus* which lacks these characteristics (see Plates 4-5). Although young *C. nelsoni* lack rump spines, they still may be recognized easily from adult or young Chihuahuan pocket mice by the presence of white subauricular spots and dusky plantar surfaces of the hind feet.

MATERIALS AND METHODS

This investigation was divided into four major phases: (1) preliminary field work, (2) habitat selection, (3) home range and population dynamics and (4) dissection of pocket mice to determine reproductive condition.

Galvanized iron Sherman live traps, 25 cm long and 7.5 cm square in cross section, were used for trapping. The traps were baited with chicken scratch composed of maize, wheat, and barley. Live traps were used because snap traps are ineffective for capturing *Perognathus merriami* (Bailey 1905) and traps were needed that would capture all three species of pocket mice with equal efficiency. During the summer, traps were set in shade. In the absence of natural cover, cardboard covers were used. Traps were inspected and animals removed before 1000 h. Each individual was marked by clipping a combination of two toes.

Plate 3. Merriam's pocket mouse, *Perognathus merriami*, from Big Bend, 1958. Fluff grass (*Dasyochloa pulchella*) in the background. Photograph by R. D. Porter.

Plate 4. Chihuahuan pocket mouse, *Chaetodipus eremicus*, from Big Bend, 1958. Ground cholla (*Opuntia schottii*) in the background. Photograph by R. D. Porter.

Plate 5. Nelson's pocket mouse, *Chaetodipus nelsoni*, from Big Bend, 1958. Note the prominent rump spines. Lechuguilla (*Agave lechuguilla*) in the background. Photograph by R. D. Porter.

Preliminary Field Work

Preliminary field investigations were conducted to determine the most efficient trap interval and best means for eliminating "trap addiction" of individual mice. Tests indicated that traps placed at 10-m or 12-m intervals gave equally good indications of population size, whereas a 15-m interval with a resultant smaller number of traps gave a poorer estimate of the population. An analysis of the number of sites at which individual mice were trapped indicated that a distance of 15 m approached the maximum distance between traps for the purpose of determining the movements of pocket mice, and that a 10-m interval was best for collecting data on home range and movements under the prevailing conditions (Porter 1962).

During the trap-interval tests it was noted that many of the mice were recaptured at the same sites. This "addiction" to certain traps not only restricted the movements of the mouse so that the extent of its home range could not be determined (Chitty 1937), but also excludes other individuals from being captured at the site (Chitty and Kempson 1949; Miller 1958). To avoid these difficulties, a system of rotating the traps was devised and tested. The rotation system proved effective in eliminating trap addiction (Porter 1962).

The Habitat Plots

To compare habitat preferences and obtain specimens of the three species of pocket mice, 76 small "habitat plots" of 0.4-0.8 ha were live-trapped in a variety of vegetation and substrate types. For most plots, the distance between traps was approximately 12 m. The number of traps per plot ranged from 14 to 85, with an average of 42. A total of 17,382 trap nights were compiled on the plots. Each plot was trapped for an average of 6.3 nights. The pocket mice captured on these plots were weighed and their reproductive tracts were removed for study.

The Population Plots

To study home range and population dynamics, three plots 148.5 m square (2.2 ha) were constructed at three of the sites analyzed as habitat plots. Each plot contained 784 trapping stations 5.5 m apart in a 28 x 28 grid (Fig. 7). The plot corners were staked with rebar and each of the remaining 780 trapping stations was marked with a wooden stake. Throughout the plot, each stake was marked alternately with orange or red tape in one row, and white or yellow tape in the next row (Fig. 7). Each 2.2-ha plot was located in a habitat which supported predominately one of the three species of pocket mice. The plot for the study of Chihuahuan pocket mouse populations was west of the Marathon highway, 1.6 km south of the upper Tornillo bridge at an elevation of 864 m (Figs. 2, 8; Plate 6). Population studies of Merriam's pocket mice were performed at a plot west of the Marathon highway, at Panther Junction and southeast of Lone Mountain at an elevation of 1,127 m (Figs. 2, 9; Plate 7). The third plot, selected for the study of Nelson's pocket mouse, was located west of the Glenn Spring road 1.6 km south of the junction with Boquillas highway at an elevation rang-

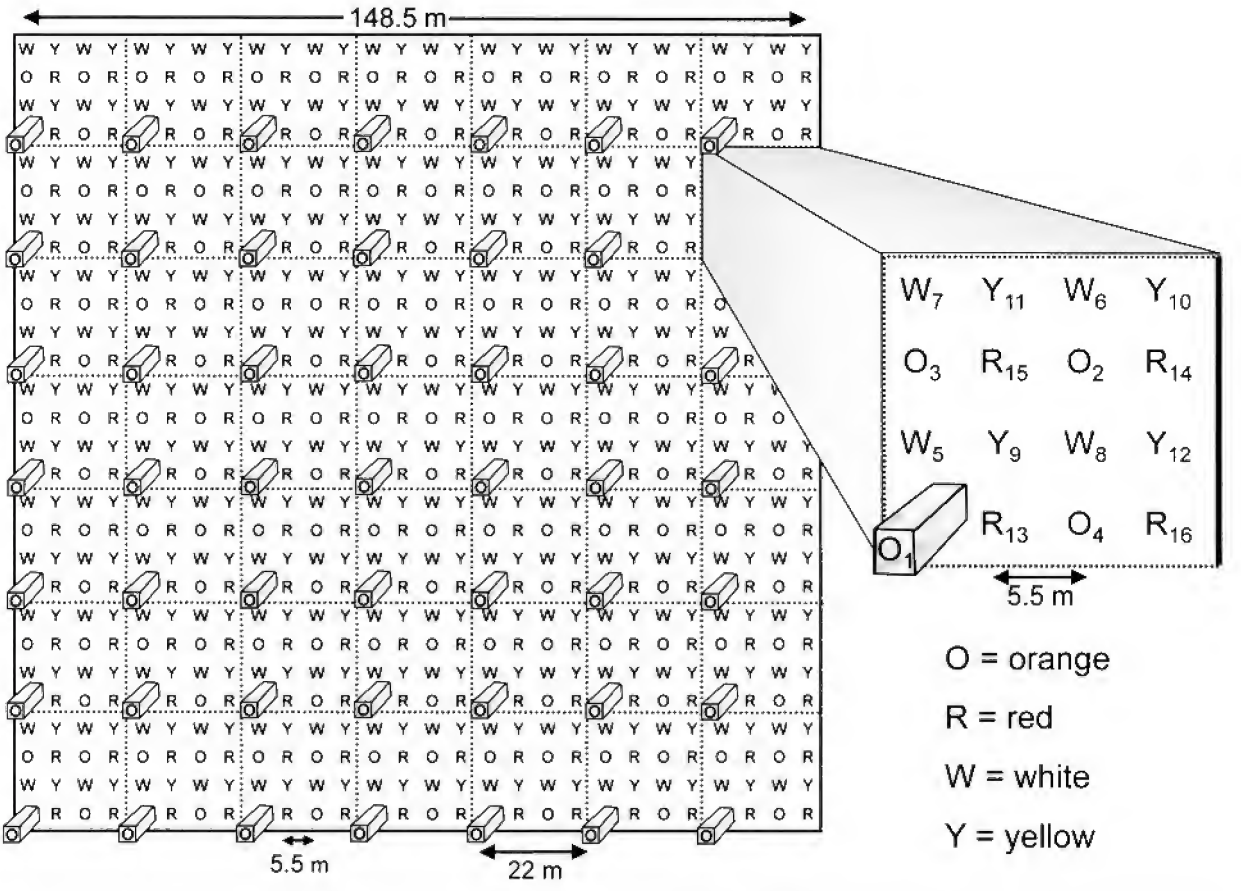

Figure 7. Layout and trap rotation scheme for the population plots. The left square shows the entire 2.2-ha plot. Letters represent the 784 trapping sites each marked in the field by a stake with a colored flag. Only 49 traps were set on a given night and each site was trapped for a single night during the 16-day trapping period. The placement of the 49 traps for the first night of the trapping period is marked on the figure by a trap at an orange stake. On subsequent nights of the trapping period, each trap was systematically rotated through the 16 trap sites delimited by the dashed lines marked on the grid, always maintaining a distance of 22 m between traps. Subscript numbers 1-16 in the enlarged section represent the rotation sequence of a single trap through 16 nights, beginning with the four orange sites, followed in sequence by the white, yellow, and red trap sites.

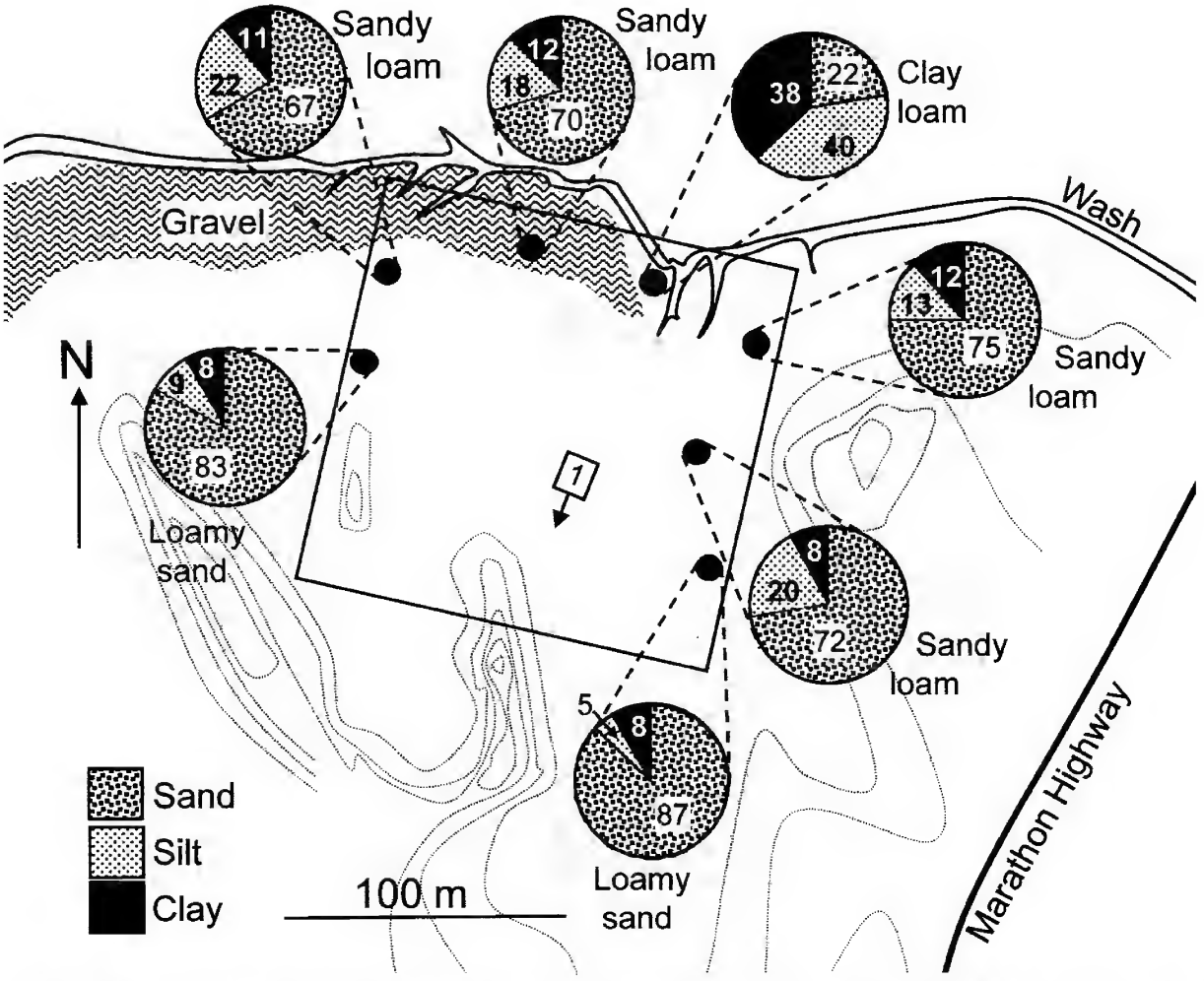

Figure 8. The Eremicus plot in relation to surrounding features. The plot is indicated by the square. Black circles indicate soil sample locations. Circle graphs show percentages of sand, silt, and clay in each sample, with soil classifications indicated. The number enclosed in the square indicates the percentage gradient at that location, and the arrow indicates the direction of the uphill slope. Contour intervals represent approximately 1 m elevation, beginning with the level of the plot. Elevated areas in the plot are sandstone outcrops about 1 to 1.5 m above the general elevation of the plot. UTM coordinates of corner stakes located in 2008 are as follows: southeast corner 13-679981E 3253996N; southwest corner 13-679835E 3254029N; northwest corner 13-679865E 3254171N.

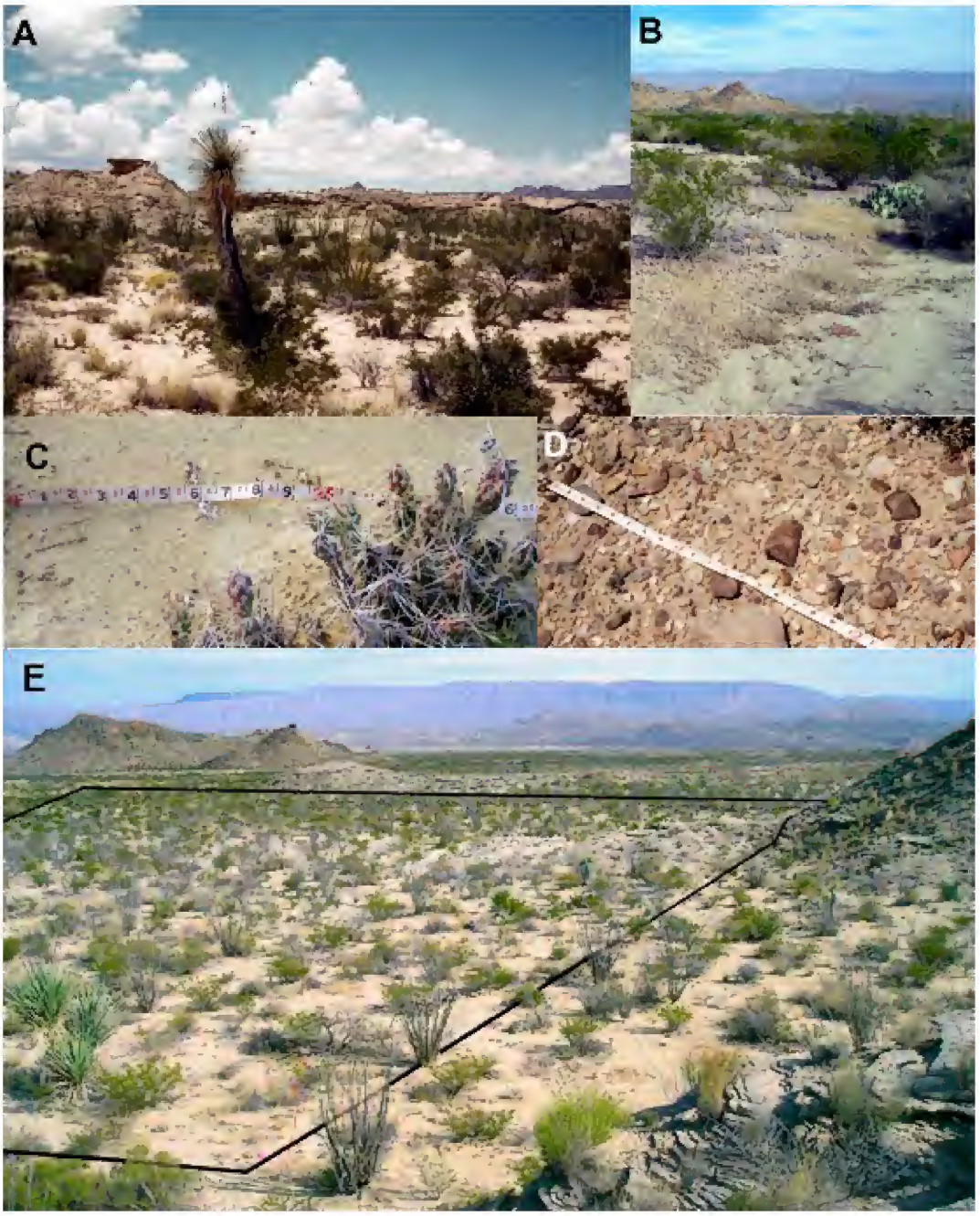

Plate 6. Eremicus plot, rock-free flats habitat. A. Looking southeast towards the bluffs just beyond the southern edge of the plot. *Yucca elata* is in the left foreground. Creosotebush (*Larrea tridentata*) is the dominant plant in the foreground; ocotillo (*Fouquieria splendens*) in the background. B. Looking north along the boundary of the gravelly and non-gravelly portions of the plot showing the area of clay loam soil (Fig. 8). The vegetation (mostly creosotebush) in the middle distance marks the location of the wash. C. Rock-free sandy loam soil characteristic of the majority of the Eremicus plot. *Opuntia schottii*, the most abundant understory species, is visible in the photograph. The scale shown in this and other plates is graduated in tenths of feet (3.0 cm). D. Surface rocks at the northern edge of the plot. E. Southwestern corner of the plot looking northeast. Photographs A and D by R. D. Porter, Spring 1960. Photographs B, C, and E by C. A. Porter, November 2008.

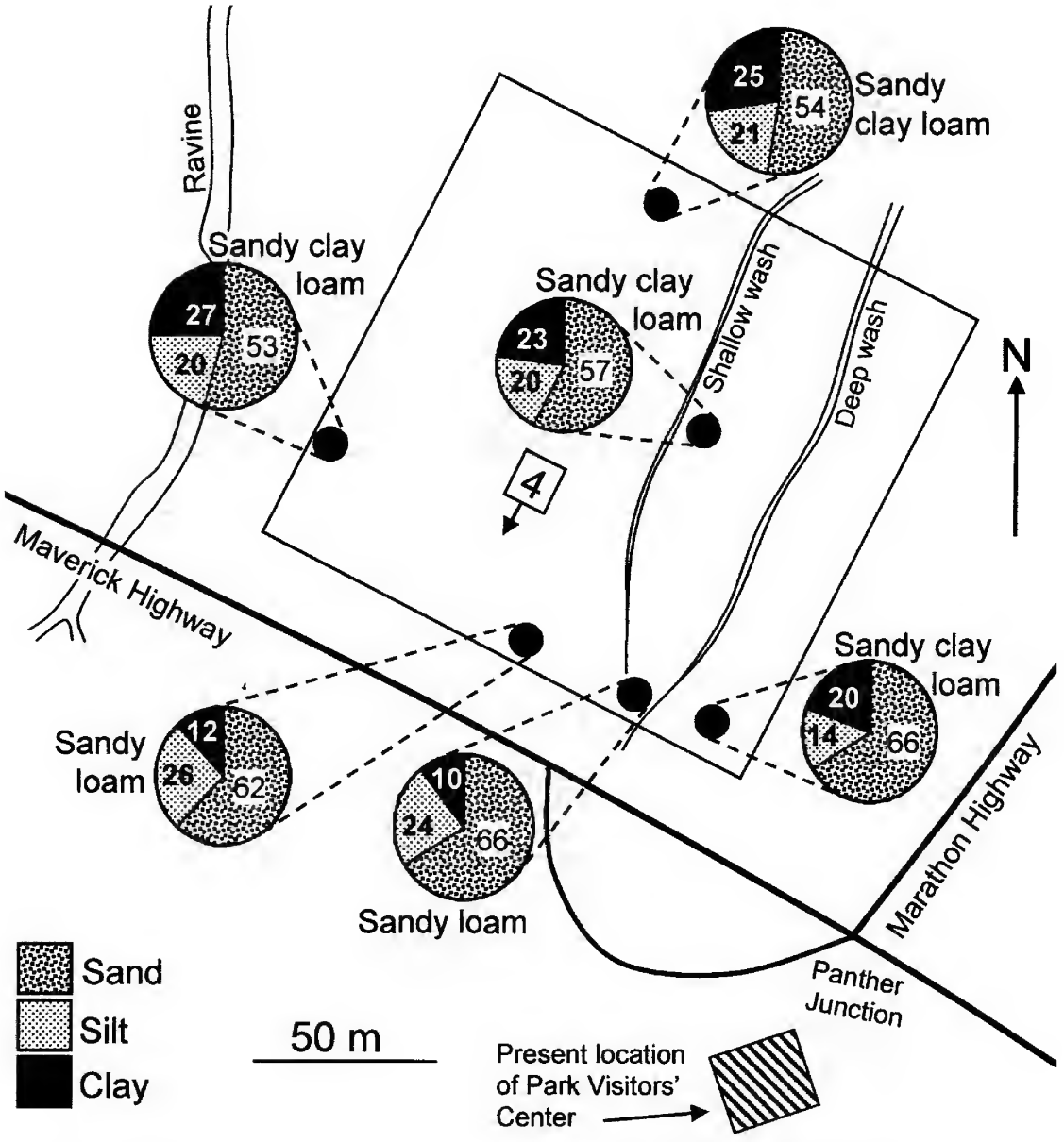

Figure 9. The Merriami plot in relation to surrounding features. The boundaries of the plot are indicated by the square. The easternmost corner of the plot is at UTM 13-674237E 3245884N. Since only one corner stake was located, the orientation of the plot is approximate, but is inferred from physical evidence at the site, and from the description in Porter (1962). Black circles indicate soil sample locations. Circle graphs show percentages of sand, silt, and clay in each sample, with soil classifications indicated. The number in the square indicates the percentage gradient, and the arrow indicates the direction of the uphill slope. The "deep" wash is approximately 45 cm deep.

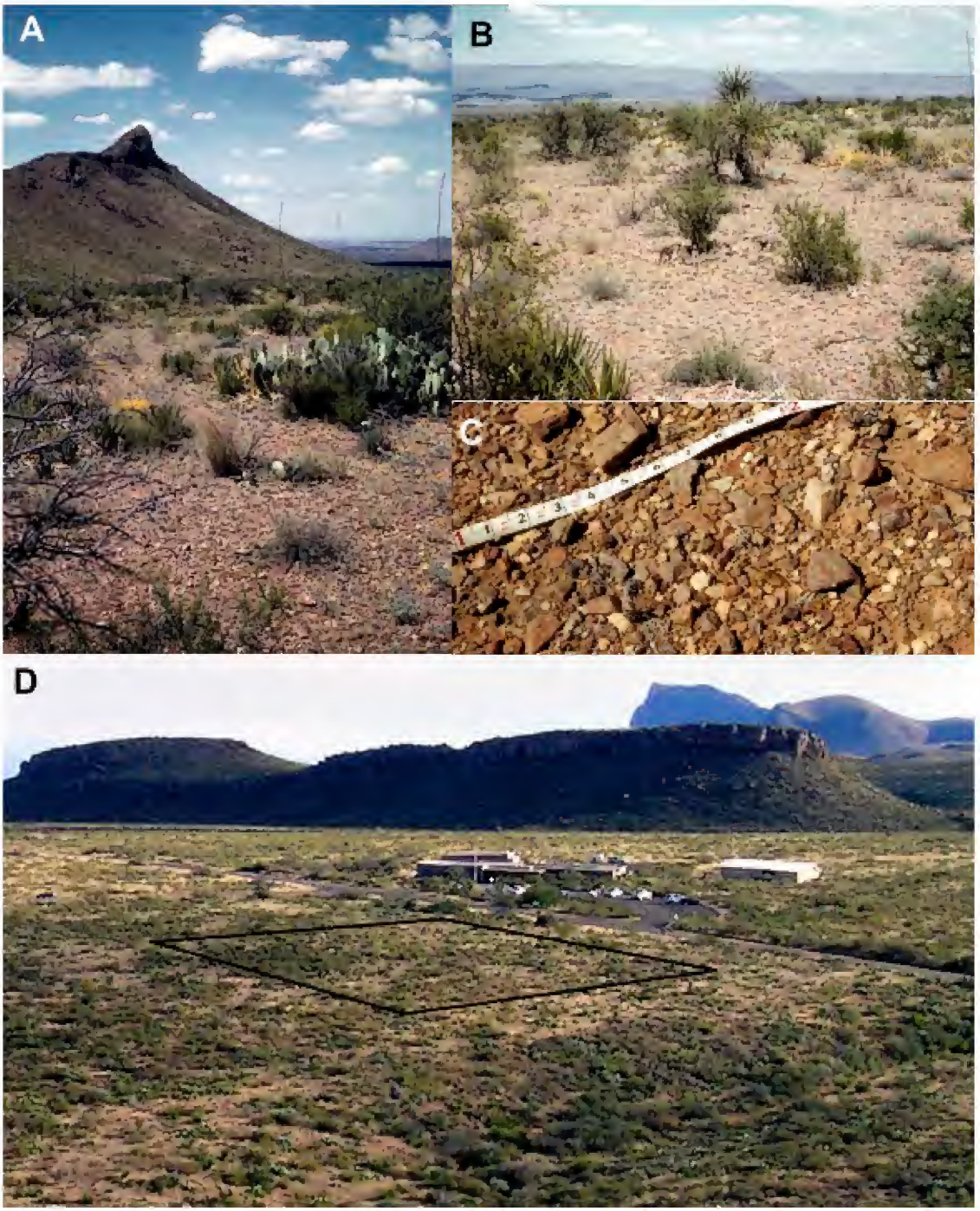

Plate 7. Merriami plot, fine gravelly foothill habitat. See front and back cover for an additional view of this plot. A. Looking northwest towards Lone Mountain. Engelmann's prickly pear (*Opuntia engelmannii*) is visible to the right. B. Looking east; Lechuguilla (*Agave lechuguilla*) in left foreground; Torrey's yucca (*Yucca torreyi*) in background; tarbush (*Flourensia cernua*) in between. Note the very small clumps of fluff grass (*Dasyochloa pulchella*) in open areas that result in a high density of understory plants while still maintaining minimal ground cover. C. Surface rocks. D. Merriami plot at Panther Junction seen from the ridge of Lone Mountain looking south-southeast. The structures beyond the plot are the Park Visitors Center and Headquarters buildings. Photographs A-C by R. D. Porter, Spring 1960. Photograph D by C. A. Porter, November 2008.

ing from 959 to 977 m (Figs. 2, 10; Plate 8). The three plots were used from March 1958 through July 1959 in a mark-and-recapture study of population dynamics and home range size. Hereafter these three plots will be referred to collectively as the "population plots" and individually as the "Eremicus," "Merriami", or "Nelsoni" plot.

In 1958 the population plots were trapped simultaneously for four periods of 16 days each (4 March to 8 April; 5-29 July; 4 September to 7 October; and 11-29 December). In May and July 1959, they were trapped for only eight days each period (12-24 May and 7-13 July) except for the Nelsoni plot which was trapped for 16 days in May (12-31 May). The 16 or 8 days were not always consecutive and the interval between trap nights was not the same for each period. The March-April and September-October trapping periods will hereafter be referred to simply as March and September periods.

On each population plot, one-sixteenth (49) of the 784 trap sites was trapped each night, with the 49 traps being rotated systematically to a new site each night of the 16-day trapping period, until all 784 sites were trapped for one night each. Within the plot, each trap was rotated through a 4 x 4 grid of 16 trap sites as shown in Fig. 7. For any one night, the distance between traps was always 22 m and each trap was rotated at least 5.5 m and usually 15.6 m or 11 m from where it had been placed on the previous night (Fig. 7). Consequently, each of the 784 sites was sampled only once during each 16-day trapping period. Therefore, it was impossible for an individual to be captured more than once at a unique trap site during a single trapping period.

Miller (1958) used a rotational system which differed from mine in that he selected sites randomly rather than systematically. Under conditions of this study, random selection of sites would have complicated the setting of traps to such an extent that the amount of time involved in moving traps would have rendered the method impractical. Furthermore, if all traps had been placed randomly, a set distance between traps could not have been maintained.

This rotational method of trapping has the following advantages over methods of stationary trap arrangement: (1) Because mice are not captured at the same trap site twice, the extent of home ranges may be ascertained with fewer captures. (2) A more complete coverage of the plot is accomplished. (3) A better estimate of the population size is possible. Hayne (1949) reported that trap addiction tends to underestimate the size of the population when population estimates are based on the Lincoln Index because traps which consistently capture the same animals have a much higher probability of capturing a particular animal than do other traps. (4) Stickel (1960) has shown that during periods of low population density the home ranges of animals increased in size and with an increase in population the reverse was true. She pointed out that a trapping area may be large enough to enclose the ranges of several mice when home ranges are small and of only one mouse when home ranges are large. As a result she believes that it may be necessary to set traps closer together when ranges are small than when ranges are large. Stickel (1960) also pointed out that with larger intervals between traps (with a resultant decrease in number of traps) a higher percentage of animals was captured in only one trap. She also indicated that the scarcity of traps probably prevented capture of some mice. The rotational system tends to alleviate these problems by eliminating trap addiction and by bringing about a more random distribution of captures. Thus it probably lessens the need to change the distance between traps to correspond with the size of the home range. (5) A more random capture of animals is accomplished by the use of this method since mice have to search out the new location of the trap each night if they do not encounter it accidentally.

Habitat Analysis Methods

Analysis of Vegetation.—Substrate and vegetation were studied on the three 2.2-ha population plots and on selected habitat plots chosen to include those having predominately one species of pocket mouse and also those plots having combinations of two or three species.

The point-centered quarter method (Cottam and Curtis 1956) was used for vegetational analysis. Cottam and Curtis (1956) found that this method was generally superior to the other distance methods studied. Although the method normally is not applicable

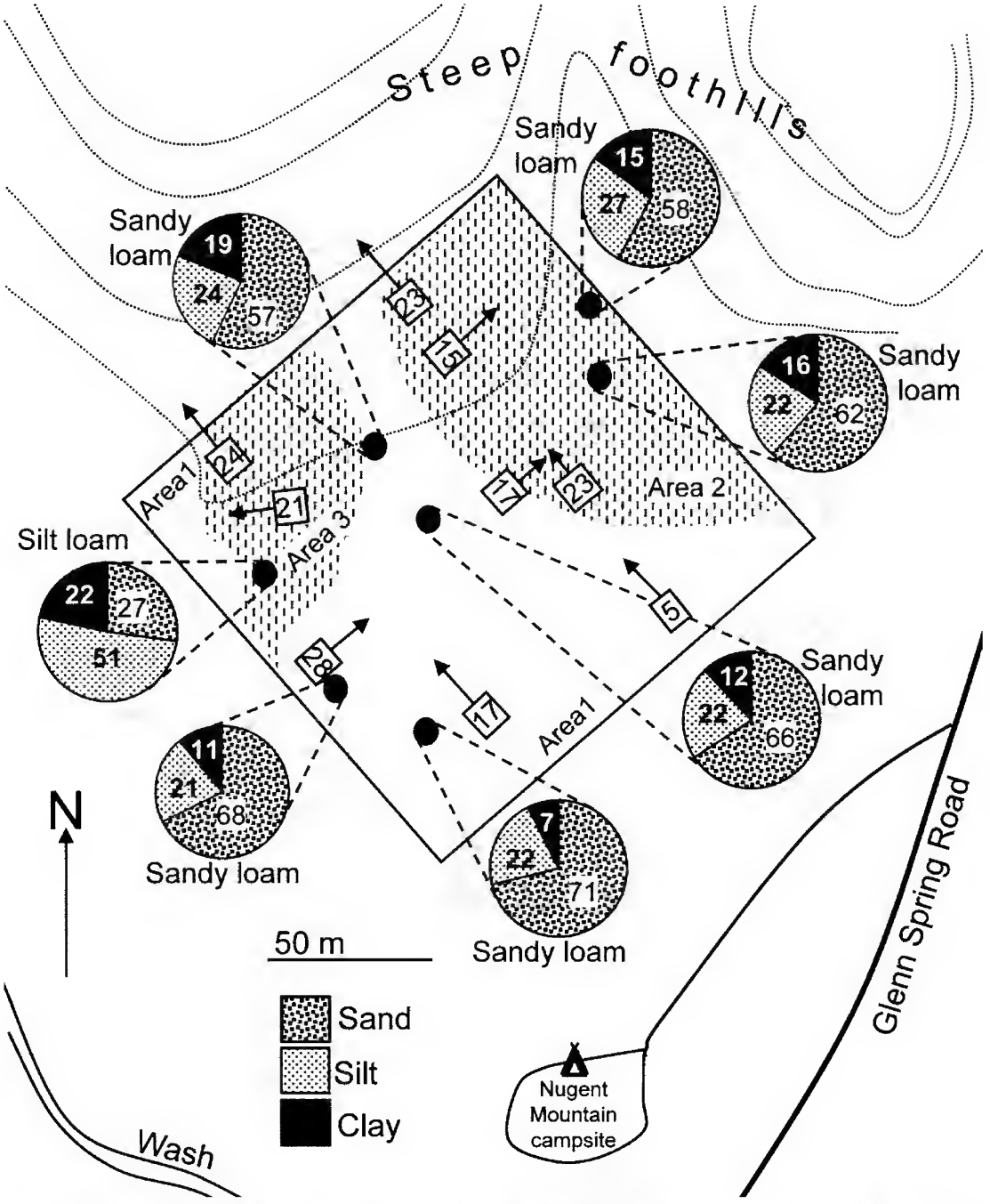

Figure 10. The Nelsoni plot in relation to surrounding features. The plot is marked by the large square. Black circles indicate soil sample locations. Circle graphs indicate percentages of sand, silt, and clay in each sample, with soil classifications indicated. The numbers in squares indicate the percentage gradient, and the arrow indicates the direction of the uphill slope. The shaded areas in the plot designate substrate areas 2 and 3 (see text). The present location of a backcountry campsite is indicated. Metal stakes marking the south (UTM 13-679447E 3237900N) east (13-679559E 3238000N), north (13-679457E 3238098N), and west (13-679345E 3238004N) corners of the plot were located during field work in 2008.

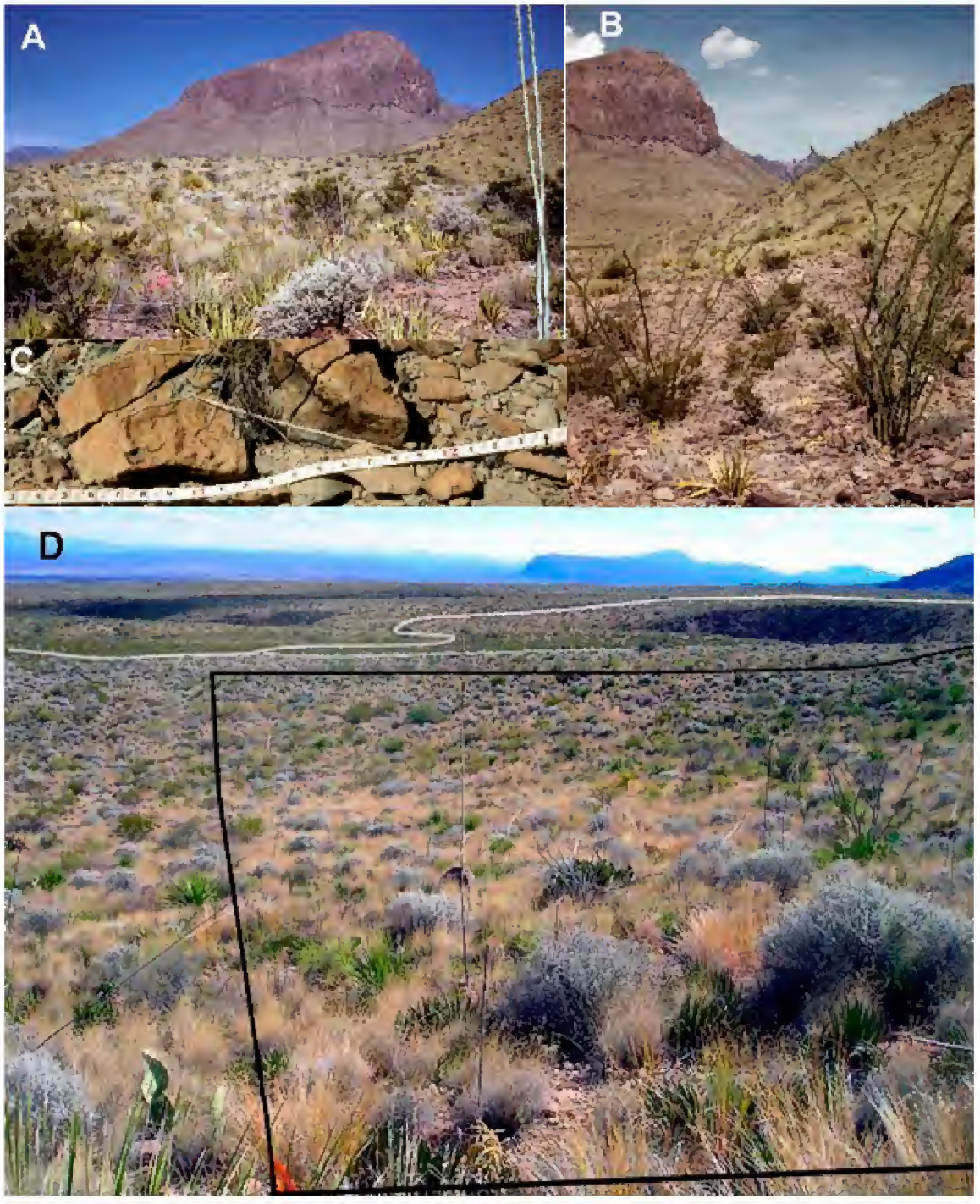

Plate 8. Nelsoni plot, coarse stony mountainside habitat. A. Lechuguilla (*Agave lechuguilla*) and chino grass (*Bouteloua breviseta*) in foreground. Nugent Mountain is in background. B. Area of Nelsoni plot which is underlain by shale (Area 3). Note relative paucity of understory vegetation in this area and presence of ocotillo (*Fouquieria splendens*). C. Surface rocks. D. Looking southeast from the northern corner of the plot. Area 2 is in the foreground; Area 1 is in the distance. The white lines beyond the plot show the location of the Glenn Spring Road and the present entrance to the Nugent Mountain backcountry campsite. Photographs A-C by R. D. Porter, Spring 1960. Photograph D by C. A. Porter, November 2008.

to non-randomly distributed vegetation such as usually occurs in the desert, sufficient randomness seemed to prevail empirically (Table 1). Additionally, less time was involved in collecting vegetational data by use of this method than by more conventional methods because dimensional plots were not needed. Wallmo (1960) used this method to determine the density of desert scrub in the Big Bend area and believes that it gives a reasonable estimate of plant density in desert scrub.

At selected points, measurements were made to the closest understory, overstory and annual herbaceous plant in each of four quarters around the point. A device designed to randomize the compass position of the quarters was driven through the loop of the measuring tape at each point and the bisector whirled and allowed to come to a stop. Illustrations of the device and its use are given in Porter (1962).

On the 2.2-ha population plots, plants which were of a height that the canopy did not inhibit movements of pocket mice were regarded as overstory. Hence prickly pear (subgenus *Platyopuntia*), krameria (*Krameria*) and leather plant (*Jatropha dioica*) were considered understory plants on these plots (Appendix I), but as overstory on the habitat plots. The population plots were analyzed a second time in conjunction with the habitat plots, but the second time these three types of plants were considered as overstory plants for comparison. There was little change in the density of vegetation and in species composition as a result of the shift in classification.

The average measurements of each of these categories were converted to plants/acre by dividing 43,560 by the square of the average distances (Cottam and Curtis 1956). The resulting plant density values were then converted to plants/m^2, which is the unit reported in this publication. The relative density and dominance of plant species were determined by the following formulae (Cottam and Curtis 1956).

$$\text{Relative density} = \frac{\text{Number of individuals of this species}}{\text{Number of individuals of all species}} \times 100$$

$$\text{Relative dominance} = \frac{\text{Total basal area of the species}}{\text{Total basal area of all species}} \times 100$$

Basal area is the average area covered by an individual of the species (Appendix II); total basal area is the area covered by all individuals on the plot. On each habitat plot 16 points were established, 30.5 m apart, with a total of 64 measurements for each category or a total of 128 measurements for each plot. On the population plots, 49 points were established every 22 m at a staked trap site (Fig. 7). Hence 196 measurements were made of each category on each 2.2-ha population plot.

Cottam and Curtis (1956) regarded a standard error of less than 10% of the mean as satisfactory for most biological work and that the distance measurements needed to be squared before density could be determined. Hence, they considered that the standard error of the distance measurements be such that when they were converted to densities the plus or minus figures be within 10% of the mean density. They found that a standard error of $\leq$4.65% of the mean distance met this condition. In a hardwood forest in Wisconsin

Table 1. Statistical tests of the point-centered quarter method of vegetational analysis in desert scrub for 196 samples. The parenthetical number represents the value for 195 samples, with one unusually large distance measure omitted.

	Standard Error			Coefficients of Variation for 196 samples		
	Overstory[a]	Understory	Combined	Overstory	Understory	Combined
Merriami Plot	160	6.86	5.2	57.2	96.0	73.6
Nelsoni Plot	196	7.5 (5.8)	5.9	63.3	80.6	82.7
Eremicus Plot	160	4.97	4.97	58.1	95.6	69.6

[a]Number of measurements needed to obtain a standard error of 4.65% of the mean distance for the overstory.

Cottam and Curtis (1956) found that 40 random measurements were sufficient to give a statistically valid analysis of the density of a forest. Table 1 gives the number of measurements necessary to get a standard error of 4.65% of the mean for the two categories on the population plots. It was found that in desert scrub vegetation at least 190 measurements of overstory plants and well over 196 measurements of understory plants were needed to get a standard error as low as 4.65% of the mean.

Cottam and Curtis (1956) reported coefficients of variation of their samples in Wisconsin in the range of 24-29%. The samples I took in desert scrub vegetation were more highly variable than those taken in homogeneous hardwood forests (Table 1). Desert scrub is a heterogeneous mixture of species which apparently are less randomly distributed than are trees in a hardwood forest. Hence, the coefficients of variation in desert scrub were much higher than those obtained by Cottam and Curtis (1956). Additionally, samples taken of the overstory vegetation were less variable (more random) than those of the understory (Table 1). Although the standard errors in the analyses of desert scrub (Table 1) exceeded the arbitrary limits of Cottam and Curtis (1956), they were small enough that the differences could be distinguished between the habitats considered (Tables 2-3).

Analysis of Substrate.—The upper regolith was analyzed for soil texture (percentage of sand, silt and clay), rock content (percentage rock of various sizes), and surface rock (percentage of rock of various sizes accumulated on the surface). One or more samples (approximately one liter) of soil, 52 in all, were taken from 43 habitat plots to determine soil texture. Six or seven samples were collected from each population plot for the same purpose (Figs. 8-10). These samples were analyzed by the Bouyoucos (1936) hydrometer method. Soil texture was determined from a U. S. Department of Agriculture (1951) Guide for Textural Classification. For purposes of this study, particles <5 mm in diameter were regarded as soil; larger particles were considered to be rock. Rocks less than 7.5 cm were regarded as gravel; rocks at least 7.5 cm and less than 40 cm in longest dimension were considered cobbles; and rocks ≥40 cm were regarded as boulders. This terminology will be followed hereafter, although the dimensions differ somewhat from standard geological definitions.

Rock content was determined by digging a hole approximately 40 cm in diameter and deep enough (approximately 15 cm) to remove sufficient soil and rock to fill a 20-liter can. Samples were taken at plots where the greatest number of each species of pocket mice was captured, 60 cm from the flag marking a trapping station. The sites to be sampled were selected using a table of random numbers. From the 30 habitat plots 65 samples of soil and rock were taken; 51 samples were taken from the 2.2-ha population plots, 17 from each.

The soil was separated from the rock and weighed. To determine percentage of water a 500-gram sample of soil was removed and dried in a pan over a flame, stirring constantly until no moist soil remained attached to the spoon. The soil fraction of the total sample was then corrected for dry weight by subtracting the total weight of the water from the total weight of the sample. The rock fraction of the sample was weighed, but the water content was not determined. The dry weight of the soil fraction plus the weight of the rock fraction was the total weight of the sample. For the population plots the rock was passed through eight sieves of 5, 10, 13, 19, 25, 38, 50, and 75 mm. For the habitat plots the 10 and 19-mm sieves were not used. The rocks retained on each sieve were weighed and their percentage of the total sample ascertained.

Surface samples were taken by using a 930-cm^2 square frame at sites selected in the same manner as the soil samples mentioned above. The surface samples were sorted with the sieves mentioned previously. Sixty samples of surface rock were taken from each 2.2-ha population plot and 164 samples from 28 habitat plots. The point-centered quarter method (Cottam and Curtis 1956) was used to analyze the abundance of the boulders >40 cm in diameter on the Nelsoni plot and on four of the habitat plots.

Laboratory Examinations

A total of 633 specimens of the three species of pocket mice (*P. merriami*, 216; *C. nelsoni*, 196; *C. eremicus*, 221) was removed from the habitat plots. In the laboratory the mice were placed alive in a plastic bag and weighed on a balance calibrated to 0.1 g. Cotton soaked in chloroform was placed in the bag and ectoparasites were brushed from the animals and sent to the Texas Department of Health for determination.

Table 2. Comparative density and mean height of plant cover on the population plots. Understory plants are those for which the canopy does not inhibit the movement of pocket mice.

	Plant Density (plants/m^2)			Height (cm)	
	Overstory	Understory	Annual Herbs	Overstory	Understory
Merriami Plot	0.489	0.854	25.628	56	20
Nelsoni Plot	0.242	4.047	1.779	71	38
Eremicus Plot	0.164	0.227	0.546	79	15

Table 3. Comparative dominance based on basal area of plant cover on the population plots.

	Percent of Area Covered	
	Overstory	Understory
Merriami Plot	5.8	46.8
Nelsoni Plot	2.8	82.8
Eremicus Plot	3.0	4.3

Standard mammalogical measurements were made of each specimen prior to autopsy. An analysis of weights and measurements with regard to molting and reproductive condition is given in Porter (1962).

The reproductive tract was removed and, except for the right testes of the males, placed in a solution of formalin-alcohol-acetic acid. The right testis of each male was cut in half and a smear made on one half of a microscope slide. A smear of the right epididymis was made on the other half and the presence or absence of spermatozoa was noted. Uteri were examined for embryos and placental scars before being placed in the preservative.

CHARACTERISTICS OF THE POPULATION PLOTS

Merriami Plot.—The Merriami plot was located on an alluvial bench near Lone Mountain (Fig. 9; Plate 7) and had a gradient of only 4%. Young cottontails (*Sylvilagus audubonii*) were trapped infrequently on the Merriami plot, and pocket gophers (*Thomomys bottae*) were present. The soil was shallow, moderately permeable, and consisted of a brown, fine gravelly sandy clay loam about 35-45 cm deep overlying a gravelly outwash. Two shallow washes (<50 cm in depth) ran through the plot. The soil in and adjacent to these washes was sandy loam, deposited there by the action of flood waters (Fig. 9). 56% of the substrate material, by weight, was gravel and cobbles (Fig. 11; Plate 7C), with 0.9 cobbles (rocks 7.5 to 40 cm in diameter) per 20-liter substrate sample, and 0.6 surface cobbles per square meter.

Neither the plants of the overstory nor those of the understory were dense on the Merriami plot (Plate 7; Table 2). Although understory plants were nearly twice as numerous as overstory plants, the former covered about eight times more area (Table 3). The most notable species of the overstory included tarbush (*Flourensia cernua*), tasajillo (*Opuntia leptocaulis*), and Torrey's Yucca (*Yucca torreyi*), with yucca being less abundant (Appendix I) but more dominant based

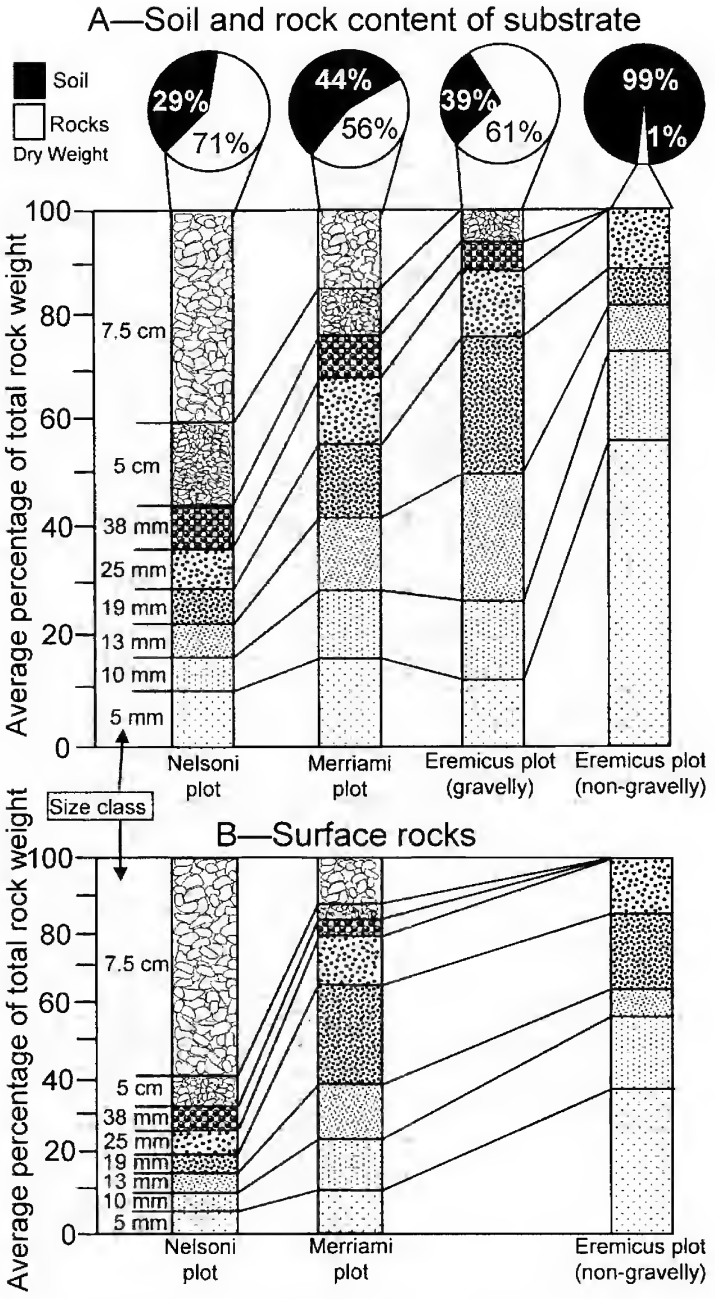

Figure 11. Average composition of substrate samples from each 2.2-ha population plot. Rocks between 7.5 and 40 cm in diameter are regarded as cobbles. Part A shows surface and subsurface cobbles, gravel, and soil to a depth of approximately 15 cm. Part B shows surface rocks only. The bar graphs show the average proportions of each of eight size classes of rocks expressed as a percentage of the total rock weight. Circle graphs show the average percentage of rocks by dry weight of substrate, including the gravelly and non-gravelly portions of the Eremicus plot.

on basal area (Appendix II). Lechuguilla, fluff grass, krameria and Engelmann's prickly pear (*Opuntia engelmannii*) were the most abundant understory species (Appendix I). Overall, the most abundant plants on the plot were lechuguilla, fluff grass, and krameria (Table 4). As a result of heavy precipitation during the fall of 1958 and the spring of 1959 (Figs. 5-6) an unusually large number of short herbaceous annuals, particularly bladderpod (*Lesquerella argyraea*), invaded the plot (Table 5).

Nelsoni Plot.—The Nelsoni plot, situated on the lower east-facing slopes of foothills of Nugent Mountain varied in gradient from about 5 to 28% (Fig. 10; Plate 8). Pocket gophers (*T. bottae*) were present on the plot. This plot had three distinct substrate types (Fig. 10; Plate 8): (Area 1) very shallow, stony sandy loam underlain by igneous parental material (Brewster stony loam); (Area 2) grayish-brown gravelly sandy loam, slope materials, 15-76 cm deep, overlying igneous parental material, and with a thin layer of calcium carbonate caliche several centimeters below the surface; (Area 3) white-colored, weathered red shale lying over a deposit of nearly pure reddish-brown calcareous shale. This portion of the plot is characterized by the presence of ocotillo and by a less dense understory (Plate 8B). Laboratory analyses indicated the soil in Area 3 to be a silt loam (Fig. 10). Igneous rock fragments were present on the surface (Plate 8C).

Over 70% by weight of the substrate on the Nelsoni plot was gravel and stones 5 mm or larger. Cobbles 7.5 cm in diameter or larger made up 40% of the weight of the substrate rock and 60% of the samples of surface rocks (Fig. 11). An average of four cobbles per 20-liter sample; about 617 boulders (40 cm or larger) per hectare (that is, one boulder per 16 m^2); and 8.15 cobbles per square meter of surface occurred on the Nelsoni plot.

The Nelsoni plot was densely vegetated (Tables 2-3) with understory plants (Table 4; Plate 8) such as lechuguilla (Plate 9) and chino grass (Plate 8D). Density of the overstory, however, was sparse (Tables 2-3). Four species of plants of the overstory were about equally abundant (Appendix I), namely, ceniza (*Leucophyllum*) feather dalea, sotol, and Gregg's coldenia (*Tiquilia greggii*). Although chino grass was the most abundant species on the plot, it accounted for only 8% of the total area covered by plants. The ratio of understory to overstory plants was nearly 17:1. In addition, plants of the understory accounted for 29 times more area covered than did plants of the overstory. Plants of the overstory encompassed only about 3% of the total area of the plot, whereas understory plants covered almost 83% (Table 3). Hence almost 86% of the surface area of the Nelsoni plot was covered with vegetation. The several species of annual plants recorded on this plot did not contribute appreciably to the density of the cover (Table 5). A small prostrate spurge (*Euphorbia*) was the most abundant annual. Plants of the understory and the overstory averaged 38 and 71 cm in height, respectively (Table 2). The average height of chino grass was >50 cm; that of lechuguilla, 32 cm (Appendix II).

Eremicus Plot.—The Eremicus plot was situated in a flat area (slightly over 1% gradient) surrounded by shale and sandstone bluffs 6-12 m in height (Fig. 8; Plate 6). Coyotes (*Canis latrans*) and kit foxes (*Vulpes macrotis*) were known to be present. Soil of the southern portion of the plot was composed of rock-free, pale brown calcareous loamy sands (Plate 6C). That of the northern half consisted primarily of pale brown calcareous sandy loams (Fig. 8). A wash 1.5 m wide and 1 m deep that cut through the northern edge of the plot was bordered by an area of fine gravelly sandy loam (Fig. 8; Plate 6B, D). These gravels were apparently deposited by mass wasting, as the gravelly portion of the plot is slightly elevated over the surrounding rock-free areas (Plate 6B). The soil was azonal and was underlain by clays to a considerable depth. A small area of clay loam soil had been exposed near the wash (Fig. 8; Plate 6B) by water action. The gravelly region of the plot (Plate 6B, D) is 61% gravel (Fig. 11A) and abruptly gives way (Plate 6B) to the sandy rock-free portion of the plot (Plate 6A, C) which is <1% fine gravel (Fig. 11A) and makes up the majority of the plot.

Both the overstory and the understory were sparse (Plate 6A, E) and both were about equal in abundance and dominance of the plant species (Tables 2-3). Less than 10% of the surface area of the plot was covered by plants. The most abundant plant of the overstory was creosotebush; the most dominant plant (in area covered), mesquite (Table 4; Appendix II). Although ground cholla (*Opuntia schottii*; Plates 4, 6C) was

Table 4. Percentage composition of selected species of perennial plants on the population plots, based on numbers of plants. The values do not total 100% because not all species are included. See Appendix I for the complete species list.

	Merriami Plot	Nelsoni Plot	Eremicus Plot
Ephedra	0.5	1.5	--
Bouteloua breviseta	--	41.0	0.5
Bouteloua eriopoda	1.0	--	--
Bouteloua trifida	--	1.5	--
Tridens muticus	--	1.0	--
Dasyochloa pulchella	21.0	4.0	2.0
Dasylirion leiophyllum	0.5	1.0	--
Yucca torreyi	1.0	--	--
Agave lechuguilla	22.0	34.0	4.0
Senna bauhinioides	--	--	5.0
Dalea formosa	--	1.5	--
Krameria	16.0	1.0	--
Prosopis glandulosa	1.0	--	3.0
Larrea tridentata	--	2.0	17.0
Jatropha dioica	--	3.0	--
Ziziphus	--	--	1.0
Echinocereus stramineus	--	0.5	2.0
Mammillaria	1.0	--	--
Opuntia engelmannii	4.0	--	6.0
Opuntia leptocaulis	6.0	0.5	4.0
Opuntia schottii	--	2.0	37.0
Tiquilia greggii	--	0.6	--
Flourensia cernua	1.5	--	0.5
Viguiera stenoloba	1.0	--	--
Unidentified grass	0.5	0.5	0.5
Unidentified shrubs	5.0	--	3.0

Table 5. Percentage composition of the annual herbaceous plants on the 2.2-ha population plots.

	Merriami Plot	Nelsoni Plot	Eremicus Plot
Zephyranthes longifolia	--	--	4.0
Eriogonum rotundifolium	--	--	2.0
Allionia incarnata	--	--	4.0
Lesquerella argyraea	80.0	--	--
Nerisyrenia camporum	--	15.0	9.0
Oligomeris linifolia	--	--	28.0
Dalea wrightii	--	2.0	--
Linum	0.5	--	0.9
Polygala scopariodes	--	13.0	--
Croton pottsii	--	6.0	--
Argythamnia neomexicana	--	3.0	0.5
Euphorbia	0.5	41.0	6.0
Nama	--	4.0	4.0
Verbena halei	3.0	--	--
Bahia absinthifolia	3.0	0.5	--
Bahia pedata	6.0	0.5	6.0
Baileya multiradiata	0.5	3.0	24.0
Dyssodia	--	4.0	10.0
Iva ambrosiifolia	3.0	1.0	--
Melampodium leucanthum	0.5	7.0	--
Parthenium confertum	--	--	1.0
Psilostrophe	--	2.0	--
Unidentified	0.5	7.0	--

Plate 9. Lechuguilla (*Agave lechuguilla*) is a common understory plant in areas occupied by *Perognathus merriami* and *Chaetodipus nelsoni*. Photograph by C. A. Porter, May 2008.

most abundant in the understory (Appendices I-II), Engelmann's prickly pear was the most dominant (Appendix II). The most abundant species were ground cholla and creosotebush (Table 4). The density of annual herbs was only slightly greater than that of perennial shrubs (Table 2). Desert marigold (*Baileya multiradiata*) and *Oligomeris linifolia* were the most abundant annuals (Table 5).

The Population Plots, 1958-2008.—Heavy grazing was permitted in the Park area until 1 January 1945 and the vegetation in many areas became severely depleted (Baccus 1971). Beginning in 1945, the National Park Service made successful efforts to aid recovery of native vegetation (Maxwell 1985). My original (1958-1959) analysis of plants on the population plots was performed less than 15 years following the establishment of the national park and the subsequent vegetational recovery. According to Warnock (1970), the effects of overgrazing in desert scrub can persist for decades and the processes of succession during recovery can occur slowly over many years.

The population plots were qualitatively assessed by L. G. Porter and C. A. Porter in May and November 2008. The brief qualitative observations performed in 2008 were not sufficient to assess the extent of vegetational succession on the plots. However, the data on vegetation presented in this study provide a valuable baseline for evaluating the successional changes that have occurred over the past half century on the population plots. The data already collected would make these plots an excellent location to pursue studies of long-term ecological change in the Big Bend area (Leavitt 2010).

During the 2008 survey, at least one corner stake on each plot was located, along with many of the wooden stakes which marked the trap sites (Figs. 7-10; Plate 2). A large number of wooden stakes were found on the Eremicus plot, and relatively few on the Nelsoni plot, perhaps due in part to the difficulty of locating stakes in the dense vegetation. On the Merriami plot, stakes were found only in the northern half of the plot, and some stakes apparently had been dislodged and washed north of the plot by heavy runoff. One of the southernmost stakes located on the Merriami plot had been partially burnt, suggesting that physical evidence of the southern portion of the plot may have been obliterated by efforts to control invasive vegetation growing along the highway.

Baccus (1971) reported increasing ground cover throughout BBNP during the period 1956-1969. However, based on data and photographs from my original study, L. G. Porter and C. A. Porter did not note significant changes in the topography or vegetation of the population plots during the 50 years since my initial evaluation. The soil was not examined in 2008, but the size, quantity, and distribution of surface rocks matched my descriptions and photographs (Porter 1962) in this study. The plants found to be predominating on the plots in the late 1950's are still abundant.

The plots were not trapped in 2008, but based on the apparent stability of the habitat, there is no reason to suspect that population levels of pocket mice have changed substantially on the plot. Lizards of the genus *Aspidoscelis* were observed in 2008 on the Merriami and Eremicus plots. In November of that year, cottontails were seen on the Merriami plot, and collared peccaries (*Pecari tajacu*) were observed adjacent to the plot, but no other mammals or reptiles were seen on the plots in 2008.

ECTOPARASITES

The collection of ectoparasites was incidental to other phases of the study. Specimens collected were sent to Dr. Richard B. Eads and Dr. John S. Wiseman, Texas Department of Health, for determination. Chigger mites were sent by them to Richard B. Loomis and D. A. Crossley, Jr. for identification.

Fleas.—I collected fleas from all three species of pocket mice, Merriam's kangaroo rat (*Dipodomys merriami*), the white-ankled mouse (*Peromyscus pectoralis)*, and a ringtail (*Bassariscus astutus*). The occurrence of fleas was most noticeable during the winter months. Yancey (1997) did not observe fleas on any pocket mice, although he collected throughout the winter at Big Bend Ranch State Park. However, he did note the presence of fleas on *Dipodomys merriami* in the Big Bend area (Yancey 1997)

I collected the stick-tight flea (*Echidnophaga gallinacea)* from *C. nelsoni* but not from any other rodents. This flea is a common ectoparasite of gallinaceous birds, but it exhibits little host preference (R. B. Eads, pers. comm., 16 December 1958). *Chaetodipus* has not been previously noted as a host of *E. gallinacea*. Whitaker et al. (1993) reported this flea from three species of kangaroo rats (*D. merriami, D. ordii*, and *D. spectabilis*), but not from any other heteromyids. I also found *E. gallinacea* on a ringtail (*Bassariscus astutus*) at Green Gulch. Eads and Wiseman (R. B. Eads, pers. comm., 10 January 1958) found a raccoon (*Procyon lotor*) 16 km west of Marathon (Brewster Co.) to be heavily infested with *E. gallinacea*. Both the ringtail and the raccoon also were parasitized by the flea *Pulex irritans*.

I collected a new species of flea (*Meringis agilis* Eads, 1960) from all three species of pocket mice. Fleas of the genus *Meringis* are primarily nest inhabitants, visiting the host only to feed (R. B. Eads, pers. comm., 18 March 1959) and are common parasites of kangaroo rats (Eads 1960; Whitaker et al. 1993). Although pocket mice and kangaroo rats were both abundant in the habitats sampled, I collected at least 26 specimens of *M. agilis* from pocket mice and none from *Dipodomys*. However, this flea has since been found on six individuals of *D. elator* from northern Texas (Thomas et al. 1990). Because *M. agilis* was not collected on *Dipodomys* in the Big Bend region, Whitaker et al. (1993) suggested that the species displays some host specificity, and Eads (1960) believed that pocket mice are the normal host of this flea. I collected the holotype, allotype, and all 24 paratypes of *M. agilis* during February 1958 and February 1959 (Eads 1960). The type locality of *M. agilis* is the foothills of the Chisos Mountains at Panther Junction, though the locality was previously reported (Eads 1960, Adams and Lewis 1995) as simply Panther Junction. The type host is *P. merriami* and the host of the type specimen is deposited in the mammalogy collection at Brigham Young University (BYU 6502). Although Eads (1960) did not state the depository for the type series of *M. agilis*, Adams and Lewis (1995) indicate that the holotype (USNM 65455) and allotype are deposited in the U. S. National Museum at the Smithsonian Institution.

I also collected *Meringis vitabilis* Eads 1960, another previously undescribed flea, from *Dipodomys merriami*. Eads (1960) had earlier examined one specimen of this flea collected in 1955 by Sherman Minton from a kangaroo rat in Big Bend. Minton's specimen, together with 26 individuals I collected, form the type series for *M. vitabilis* (Eads 1960). Eads (1960) deposited the type specimens of *M. vitabilis* in the U. S. National Museum. The holotype of *M. vitabilis* is USNM 65454 (Adams and Lewis 1995). The type locality (not previously published in full) is Tornillo Flat, 3.2 km south of Tornillo Creek along the Marathon Highway.

Eads (1960) did not indicate which species of kangaroo rat was the host of the paratype of *M. vitabilis* collected by Minton, but Minton informed Eads (R. B. Eads, pers. comm., 28 October 1957) that the flea was collected from *D. ordii* near the "pipeline house" on the Olin Blanks Ranch at the northern base of the Rosillos Mountains, and that the host was identified by the University of Michigan Museum of Zoology. The host data provided by Minton correspond exactly to specimen UMMZ 103322 in the University of Michigan mammal collection. As recently as February 2008, this specimen remained identified as *D. ordii*; however Priscilla Tucker (pers. comm. to C. A. Porter, 5 February

2008) examined the specimen, and found that it was *Dipodomys merriami*. Two other kangaroo rats in the UMMZ collected at Big Bend by Minton also are also *D. merriami*. It is clear, therefore that Minton's specimen was actually collected from *D. merriami*, and thus Merriam's kangaroo rat is the host of the entire type series. Eads et al. (1987) did report *M. vitabilis* from *D. ordii* collected in 1950 from Motley County, Texas, though they mistakenly credited me as the collector.

I collected six specimens of the flea *Malaraeus sinomus* from *Peromyscus pectoralis* at Green Gulch. This flea is uncommon in Texas (Eads and Dalquest 1954), but is known from a variety of hosts elsewhere (Whitaker 1968; Whitaker et al. 1993).

Sucking Lice.—The only louse found on mammals during the study was *Fahrenholzia pinnata*, collected from four specimens of Merriam's kangaroo rat in the vicinity of Tornillo Flat. This louse is common on many species of kangaroo rats and has been recorded from some pocket mice (Thomas et al. 1990; Whitaker et al. 1993; Light and Hafner 2007). Light and Hafner (2007) reported lice of this genus from *P. merriami* (in Coahuila) and from *C. eremicus* (southern New Mexico). No lice of the genus *Fahrenholzia* have been reported from *C. nelsoni*, and the pocket mice examined in this study did not host any louse species. Light and Hafner (2007) found evidence of cryptic species in lice identified as *F. pinnata*.

Ticks and Mites.—The larvae and nymphs of ticks (*Dermacentor variabilis*) were taken from all three species of pocket mouse and from Merriam's kangaroo rat. Adult stages of this tick usually parasitize carnivores (R. B. Eads, pers. comm., 18 March 1959). Whitaker et al. (1993) report *P. parvus* as the only known heteromyid host of this species.

Several species of mites were also taken. The large mite, *Androlaelaps grandiculatus*, was originally described from *P. merriami* (Eads 1951), and was by far the most common parasite found on pocket mice during this study. This species was taken from all three pocket mice and from Merriam's kangaroo rat. Other mites collected in this study include *Androlaelaps fahrenholzi* (from *C. nelsoni* and *Dipodomys merriami*) and *Echinonyssus incomptis* (from *C. nelsoni*). Three mites from Merriam's kangaroo rat were identified by Eads as an undescribed species of *Hirstonyssus* (genus *Echinonyssus* in current taxonomy). The specimens were sent to Richard W. Strandtmann (Texas Tech University) for further study, but only one specimen was an adult, and it was determined that a larger series would be needed to describe the species. Yancey (1997) found unidentified mites on all three species of pocket mice at Big Bend Ranch, and indicated that mites were typically found on the tail in *Chaetodipus*. Baccus (1971) reported that chiggers in *P. merriami* were usually concentrated in the soft tissues of the cheek pouches.

I collected chigger mites from several mammalian and avian species in BBNP. The chiggers taken from pocket mice include *Kayella lacerta* and *Euschoengastoides hoplai* (my specimens were reported by Loomis and Crossley 1963). Other chigger specimens from pocket mice were identified (R. B. Eads, pers. comm., 3 April 1959; Porter 1962) as representing two undescribed species of the genera *Trombicula* (subgenus *Trombicula*) and *Euschoengastia*. These specimens were sent by Eads to Richard Loomis (University of Kansas), and if the specimens are still in existence, they would likely be included in the extensive Loomis collection housed at the Field Museum of Natural History. There is no record that species were described from these particular specimens. Extensive subsequent studies of Big Bend chiggers have been reported by Loomis and Crossley (1963), Baccus (1971), Loomis et al. (1972), Loomis and Wrenn (1972, 1973), Whitaker and Easterla (1975), and Wrenn et al. (1976), and it is likely that the undescribed species I collected are among the species reported and described by these authors.

Euschoengastia chisosensis was reported from Big Bend by Loomis et al. (1972) and described by Wrenn et al. (1976). Loomis et al. (1972) also reported an undescribed species of *Pseudoschoengastia* from all three species of pocket mice in Big Bend. Although *E. chisosensis* has only been reported from *Peromyscus*, either of these species could have been identified in 1959 (Brennan and Jones 1959) as an undescribed species of *Euschoengastia*, and are possible candidates for the undescribed *Euschoengastia* I collected from pocket mice.

Several species of chiggers have been collected from Big Bend that were undescribed in 1959 (Brennan and Jones 1959; Loomis 1971) and plausibly could have been identified at that time as an undescribed species of *Trombicula* (*Trombicula*). These include *Hexidionis breviseta* (Loomis and Crossley 1963; Loomis and Wrenn 1972), *Otorhinophila baccusi* (Loomis et al. 1972; Loomis and Wrenn 1973), *Euschoengastoides arizonae, E. neotomae, E. loomisi*, and an undescribed species of *Euschoengastoides* (Baccus 1971; Loomis et al. 1972). The undescribed *Euschoengastoides* was provisionally named "similis" by Baccus (1971) and Loomis et al. (1972), but the species was not formally described, and since the name did not include a diagnosis, it remains a *nomen nudum*. In addition, three species of *Trombicula* were reported (Loomis and Wrenn 1972) from the bat *Mormoops megalophylla* in BBNP.

Loomis et al. (1972) and Loomis and Wrenn (1972) report 51 species of chiggers collected from in or near BBNP. These were collected from amphibian, reptilian, avian, and mammalian hosts, and include 21 specimens (reported by Loomis and Crossley 1963) of *Neoschoengastia americana* that I collected from a rock wren (*Salpinctes obsoletus*) in Oak Creek Canyon. Loomis and Crossley (1963) also report 15 specimens of *Sasacarus whartoni* that I collected from *Peromyscus eremicus* (specimen BYU 6440) at Tornillo Flat, 10 km north of Panther Junction. Baccus (1971) and Loomis et al. (1972) report the same chigger species from both *Peromyscus eremicus* and *P. pectoralis* in Big Bend. Chiggers reported (Porter 1962; Loomis and Crossley 1963; Baccus 1971; Loomis et al. 1972; Loomis and Wrenn 1972, 1973) from pocket mice in or near BBNP include *Euschoengastoides arizonae, E. hoplai, E. loomisi, E.* n. sp. ("similis"), *Hexidionis allredi, Hyponeocula arenicola, Hyponeocula* n. sp., *Leptotrombidium panamense, Kayella lacerta, O. baccusi, Pseudoschoengastia* n. sp. (from all three species of pocket mice), *Euschoengastoides neotomae* (from both species of *Chaetodipus*), *Hexidionis harveyi* (from *P. merriami* and *C. eremicus*), *Fonsecia gurneyi, Pseudoschoengastia farneri, Hexidionis breviseta* (from *P. merriami*), *Pseudoschoengastia hungerfordi* (from *C. nelsoni*), and *Euschoengastoides imperfectus*, and *Hexidionis* sp. (from *C. eremicus*).

ALTITUDINAL DISTRIBUTION OF POCKET MICE

The altitudinal distribution of pocket mice is correlated with the occurrence of suitable habitat. Hence, at a specific elevation they may be abundant in one locality and uncommon in another, depending on the nature of the habitat. In BBNP, *C. eremicus* apparently is limited in its upward distribution by the absence of deep sandy or loamy soils. Merriam's and Nelson's pocket mice, on the other hand, appear to be limited in their upward distribution by vegetational influences. The maximal altitude of *P. merriami* and *C. nelsoni* coincide with the ecotone between desert scrub vegetation and the pine-oak-juniper woodlands. For example, both of these species were trapped in small numbers at the upper end of Green Gulch at an elevation of 1,675 m on a grassy alluvial bench surrounded by sparse stands of pine, oak, and juniper where *Sigmodon* was abundant.

In the study area, Merriam's pocket mouse ranges from 580 m near the Rio Grande to 1,675 m in Green Gulch. It is most abundant on alluvial soils in the foothills of the Chisos Mountains between 1,075 and 1,220 m. Baccus (1971) reported a similar altitudinal range in BBNP. To my knowledge, the maximal altitudinal record for *P. merriami* is 1,905 m in Guadalupe Mountains National Park, Texas (Genoways et al. 1979). Baker (1956) reported *P. m. merriami* from as low as 250 m in Coahuila.

In Big Bend, I found that the altitudinal range of Nelson's pocket mouse extended from 580 m to 1,675 m, but was most abundant on the steeper slopes of the Chisos foothills near 915 m. Judd (1967) also collected the species up to 1,675 m in rocky habitat at Blue Creek Ranch, and Baccus (1971) found *C. nelsoni* in the same general attitudinal range in Big Bend, but collected the species as high as the Chisos Basin Campground at 1,700 m. Blair (1940) reported three specimens of *C. nelsoni* at 1,460 m in Limpia Canyon about 1.6 km north of Fort Davis, Texas. In Coahuila, Baker (1956) collected specimens of *C. nelsoni canescens* at elevations up to 1,460 m and of *C. nelsoni nelsoni* up to 2,060

m. In Durango, Baker and Greer (1962) reported *C. n. nelsoni* between 1,400 and 1,860 m.

In the study area, *C. eremicus* reached its greatest abundance above 760 m, but it was common up to about 910 m. It was taken in small numbers at about 1,220 m in the foothills of the Chisos Mountains. Borell and Bryant (1942) trapped Chihuahuan pocket mice at elevations up to 1,220 m in the Big Bend area, but they found them to be most plentiful below 1,070 m. Baccus (1971) reported *C. eremicus* in BBNP mostly at 560-870 m, but found specimens as high as 1,075 m. Genoways et al. (1979) collected the species up to 1,646 m in the Guadalupe Mountains. Baker (1956) took *C. eremicus* at elevations as low as 400 m and as high as 1,585 m in Coahuila. In Durango, the species was collected at 1,140-1,265 m (Baker and Greer, 1962).

POCKET MICE IN RELATION TO HABITAT

It has long been recognized that the various characteristics of substrate and topography influence the distribution of plants and animals. The close relationship between the soil and its plant cover is shown by the fact that some species of plants may be indicators of certain soil characteristics (Clements 1920; Shantz 1938). The relationship between the soil and vertebrates, however, is more indirect and complex than that between soil and plants, since the distribution of many vertebrates is related to both soil and plant cover. It was noted early in this investigation that each of the three species of pocket mouse had its peculiar requirements of substrate and vegetation. Hence, the research was directed so as to delineate these requirements, and habitat plots were sampled in a variety of habitat types (Plates 6-8; 10-16).

Hardy (1945) analyzed the influence of types of soil on the local distribution of small mammals in southwestern Utah and determined that depth of soil, degree of slope, and the chemistry and texture of soil directly influenced the distribution of certain species. These factors along with moisture content of the soil indirectly influenced the distribution of other species. Fossorial and burrowing rodents appear to be influenced by soil type more than those that live on the surface. Davis (1938), for example, found a direct relationship between soil texture, soil depth and altitude and the size of pocket gophers (*Thomomys*) in various parts of the western United States. Davis et al. (1938) found that the distribution of pocket gophers (*Geomys*) in Texas is correlated with the distribution of fine sandy loams over 10 cm in depth. Grinnell (1932) found a direct correlation between the distribution of Panoche fine sandy loam in California and the kangaroo rat *Dipodomys heermanni*.

The distribution of some non-burrowing species of rodents also is influenced directly by soil type. The canyon mouse (*Peromyscus crinitus*), the brush mouse (*P. truei*), and the bushy-tailed woodrat (*Neotoma cinerea*) are all associated with rocky habitats. The relationship between soil and habitat preference is correlated with the nesting characteristics and food storage habits of the mice. Plants influence the distribution of vertebrate animals in that they provide food, nesting sites, shelter from the elements and escape cover.

Distribution and Abundance of Pocket Mice in Relation to Slope

In southwestern Utah, Hardy (1945) found that steeper slopes usually have soils of a coarser texture than those of more nearly level areas. In Big Bend the relationship between soil texture and gradient is not always apparent because slopes are often interrupted by local differences in topography and parental soil materials. Nevertheless, the soils of the flood plains adjacent to the Rio Grande with a gradient of 1% or less are fine loams that frequently contain 40-50% silt and more than 20% clay. Most other soils in the Big Bend area are sandy loams and sandy clay loams, depending upon their locations in relation to topographic features such as mountains, hills, rock outcrops, etc.

Hardy (1945) reported that in southwestern Utah in stony soils, topsoil particles of granule gravel varied in amount according to the gradient if the parental materials were similar. In the present study a similar correlation was noted in the cobbles and gravel present at different gradients (Fig. 12).

Plate 10. Sandy wash habitat (Plot 76 near Tornillo Creek and Rio Grande). Chihuahuan pocket mouse habitat. Note the rocky ground which distinguishes this from the rock-free flats habitat. Photograph by R. D. Porter, Spring 1960.

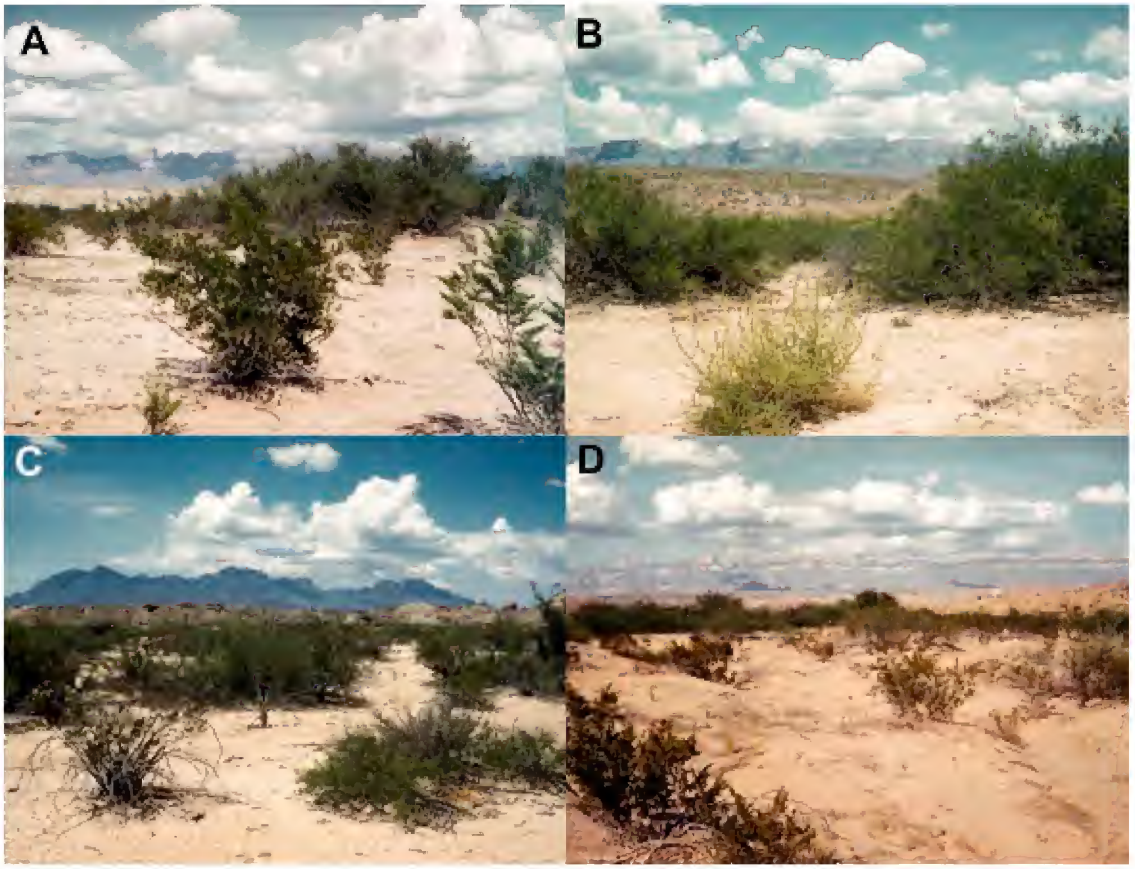

Plate 11. Rock-free flats habitat. The Chihuahuan pocket mouse was common in these areas. See also Plate 8 (Eremicus plot) for another example of this habitat. A. Plot 77, Lower Tornillo Creek, near the bridge. Sandy loam soil. Creosotebush (*Larrea tridentata*) in foreground; Sierra del Carmen of Coahuila, Mexico in background. B. Plot 78, Boquillas Village. Loam soil. Note large clumps of mesquite (*Prosopis glandulosa*) surrounded by extensive areas devoid of understory plants. C. Plot 71, Upper Tornillo Creek. Loam soil. Note clumps of mesquite surrounded by areas devoid of understory vegetation. Chisos Mountains in background. D. Plot 32, near San Vicente. Photographs by R. D. Porter, Spring 1960.

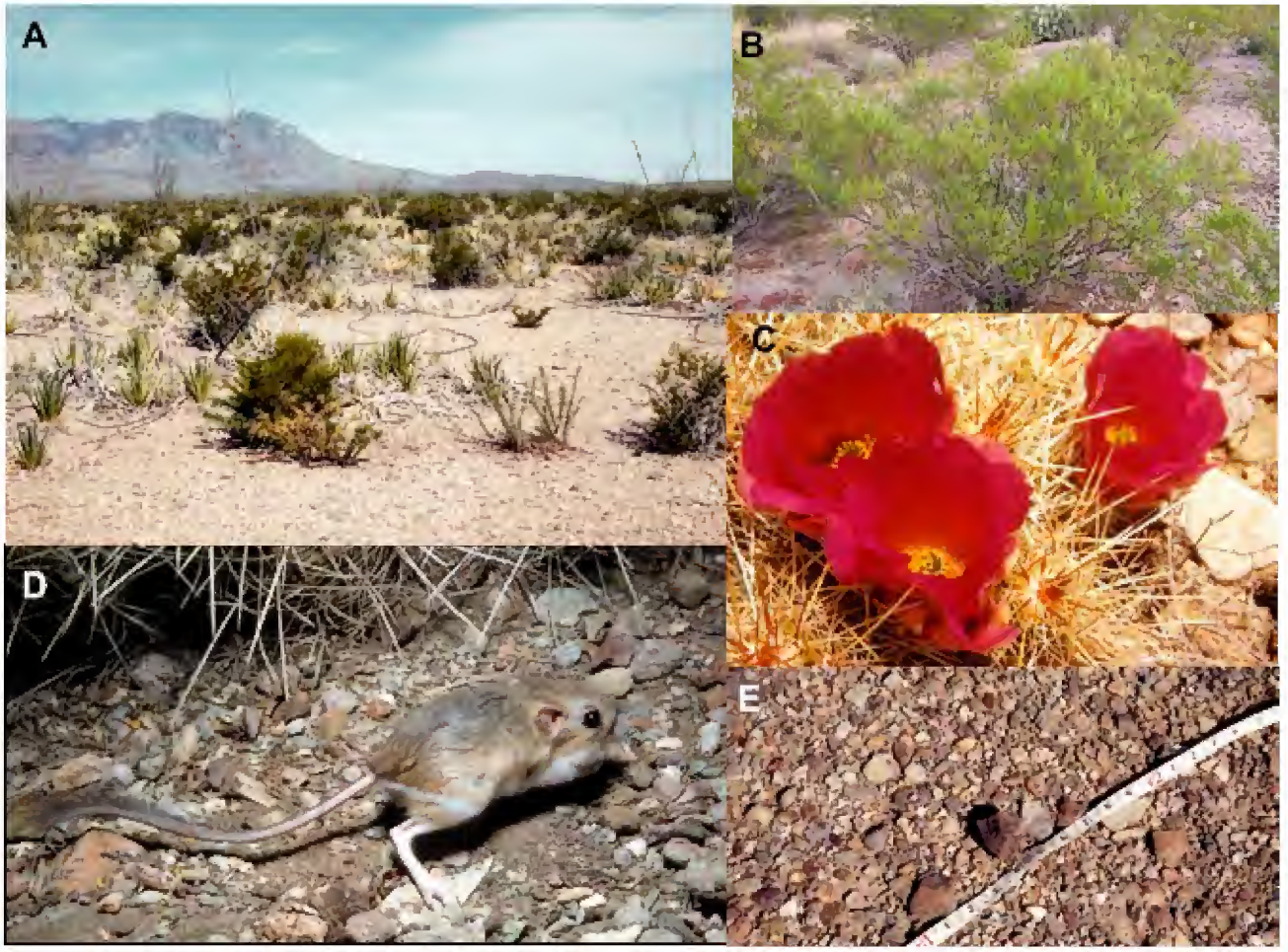

Plate 12. Fine gravelly plains habitat. This habitat differs from the fine gravelly foothills (Plate 8) in having softer soil with sparser plant cover, particularly in the understory. A. Plot 101, east of Dugout Wells. Note paucity of understory plants. Nelson's, Merriam's, and Chihuahuan pocket mice were all present. B. Creosotebush (*Larrea tridentata*) was the most abundant overstory plant in this habitat. C. Strawberry pitaya (*Echinocereus stramineus*). The understory is sparse, but is dominated by lechuguilla (Plate 9), with Strawberry pitaya and chino grass (Plate 15E) making up virtually all of the remainder. D. Merriam's kangaroo rat (*Dipodomys merriami*) reached its peak of abundance in this habitat. E. Plot 101. Surface rocks. Photographs A and E by R. D. Porter, Spring 1960; C and D by R. D. Porter in BBNP, 1958-1959. Photograph B by C. A. Porter, November 2008.

Plate 13. Fine gravelly hillside habitat. Merriam's pocket mouse was the principal species of pocket mouse in this habitat. A. Plot 62. Sotol in right foreground. B. Surface rocks, Plot 62. C. Plot 69, Maverick Junction. Note the paucity of understory cover. D. Surface rocks, Plot 69. Photographs by R. D. Porter, Spring 1960.

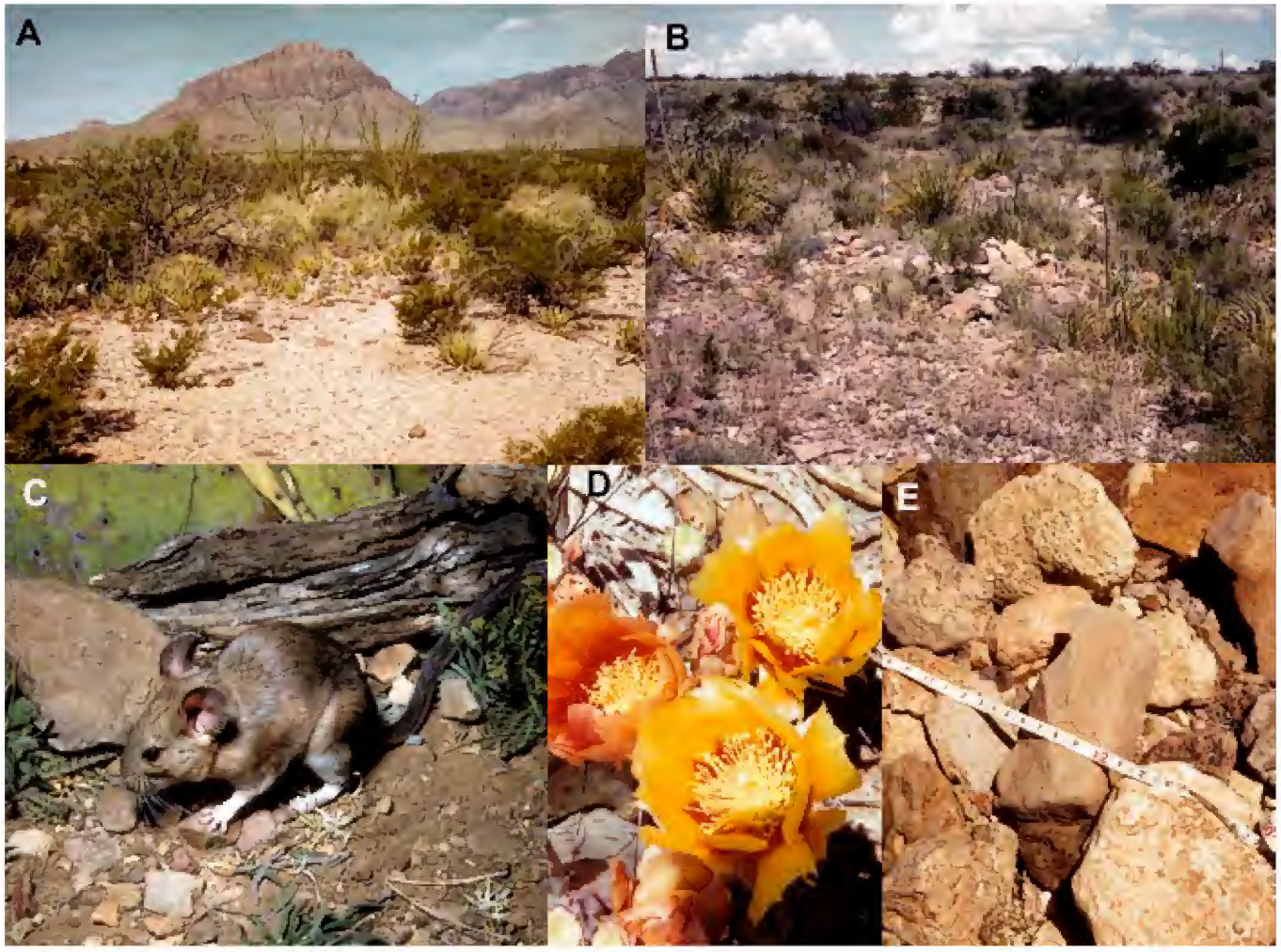

Plate 14. Coarse gravelly foothills and outwashes habitat. This habitat is characterized by an interspersion of cobbles, gravel, and sand, and of areas of dense understory cover with areas of sparse ground cover. A. Plot 38, Dugout Wells. Chihuahuan and Nelson's pocket mice were equally abundant here. B. Plot 82. Note the paucity of overstory plants, and the presence of large rocks interspersed with areas of gravel. Nelson's and Merriam's pocket mice were the predominant pocket mice on this plot. C. The white-throated woodrat (*Neotoma albigula*) reached its peak abundance in this habitat. D. Purple-tinged prickly pear (*Opuntia macrocentra*) comprises a larger percentage of the understory in this habitat than in any other. E. Plot 82. Large surface rocks are present. Photographs by R. D. Porter; A, B, and E, Spring 1960; C-D, 1958-1959.

Plate 15. Coarse stony sandy hillside habitat. A. Plot 40. Note the paucity of understory cover. Nelson's and Merriam's pocket mice were equally common on this plot. B. Surface rocks on Plot 40. C. The cactus mouse, *Peromyscus eremicus*, reached its peak of abundance in this habitat. D. Tasajillo (*Opuntia leptocaulis*) is a common overstory species in this habitat. E. Though the understory is sparse, the most abundant understory species in this habitat was chino grass (*Bouteloua breviseta*) as in other coarse rocky habitats (Plates 7, 13, 14, and 16). Photographs A-B by R. D. Porter, Spring 1960; C-D, 1958. Photograph E by C. A. Porter, November 2008.

Plate 16. Rough-broken mountainside habitat (Plot 75). A. Note large boulders and the density of understory contrasted with the coarse stony sandy hillsides shown in Plate 15. Nelson's pocket mouse was the only pocket mouse trapped on this plot. B. Surface rocks. Note Engelmann's prickly pear (*Opuntia engelmannii*) in the upper right corner. Photographs by R. D. Porter, Spring 1960.

There was correlation between slope and plant density. Slopes with a gradient of <3% had the fewest plants per square meter, whereas slopes with gradients of 3-6% and 20-30% had the most cover (Fig. 12). The high plant density on sites with gradients of 3-6% was due to an abundance of fluff grass and other small plants which covered little surface area (Appendix II). An increase in slope brought about an increase in the amount of surface area at ground level covered by plants. Steeper gradients also showed an increase in the number of plant species (Fig. 12). There was a relationship between slope and certain plant species. For example, mesquite and creosotebush were commonest on slopes of 1% or less. Plants abundant mostly on steeper slopes were chino grass, Parry's ruellia (*Ruellia parryi*), and leather plant (*Jatropha dioica*). Lechuguilla was common in all areas except where the gradient was zero to 1%, but it was most abundant on slopes of 20-26%.

The distribution of the three species of pocket mice was correlated with gradient (Fig. 13). Merriam's pocket mouse was found on a wide range of slopes, most commonly on gradients of 3-30% and reached its peak of abundance on slopes of 3-5% (Fig. 13). It occurred commonly on steep slopes providing the following conditions prevailed: (1) there was not a high percentage of large rocks (i.e., cobbles and boulders) either on the surface or in the soil, and/or (2) the understory vegetation was sparse with rather extensive bare areas interspersed with the plant cover. For example, Plot 40 (Plate 15A-B) had a gradient of 47%, relatively sparse understory (0.47 plants/m^2), and large boulders (1,852 boulders per hectare). This plot had relatively low numbers of *C. nelsoni* and *P. merriami* (0.8 and 0.6 individuals, respectively, per 100 trap nights). On the other hand, on Plot 69 (Plate 13C-D), which had a gradient of 20%, a sparse understory (0.52 plants/m^2), and few large rocks, Merriam's pocket mouse was relatively abundant (3.7 individuals per 100 trap nights). Plot 62 (Plate 13A-B; Table 6), which had similar characteristics of substrate and slope (26%) but a denser understory (9.04 plants/m^2), also supported a large population of *P. merriami* (5.4 individuals per 100 trap nights).

Nelson's pocket mouse attained its peak on gradients of 30-40% (Fig. 13). I did not find *C. nelsoni* on slopes of <1%, but it was occasionally captured on slopes of 2-10% if large rocks or dense stands of vegetation, or both, were present. For example, Plot 82 (Plate 14B, E) had a gradient of 5% and an estimated 430 boulders ≥40 cm in diameter per hectare. This plot yielded 5.6, 2.2 and 1.1 *P. merriami*, *C. nelsoni* and *C. eremicus*, respectively, per 100 trap nights (Table 6). In August 1959, another plot (Plot 101, east of Dugout Wells; Plate 12A, E) with a gradient of only 3% and fine gravelly loam (few rocks >38 mm) yielded 5.6, 10.0 and 1.1 *P. merriami*, *C. nelsoni* and *C. eremicus*, respectively, per 100 trap nights. The understory vegetation of this plot, chiefly lechuguilla and chino grass, was sparse (0.47 plants/m^2). The high population of *C.*

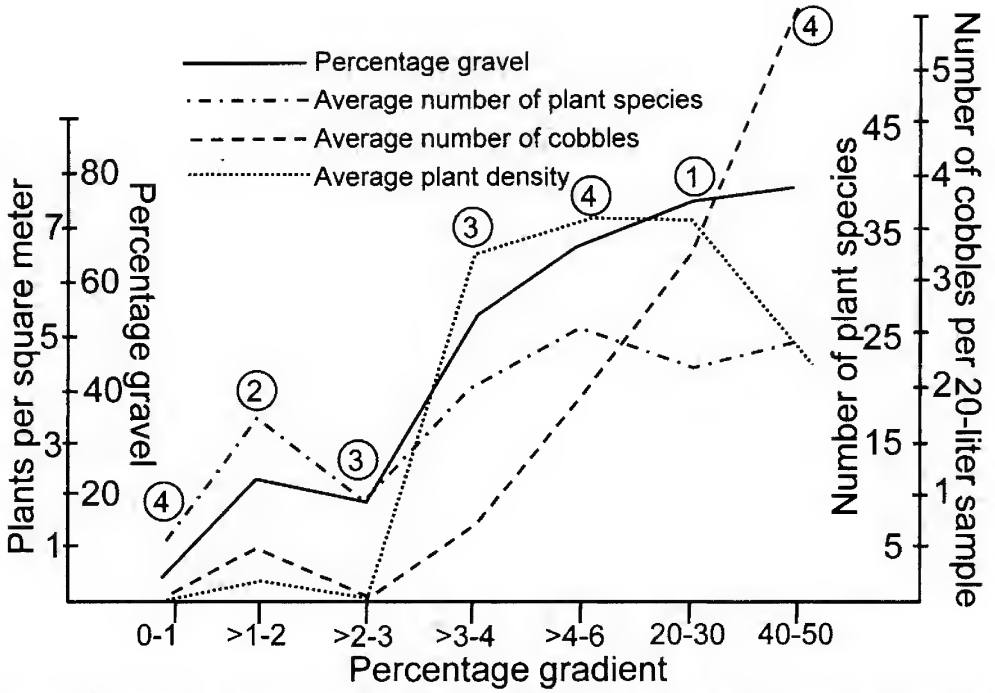

Figure 12. Percentage gradient in the habitat plots plotted against (1) plant density; (2) percentage gravel; (3) average number of cobbles (rocks 7.5 to 40 cm in diameter) per 20-liter sample of substrate; and (4) average number of plant species. Circled values indicate the number of plots sampled for each range of gradient.

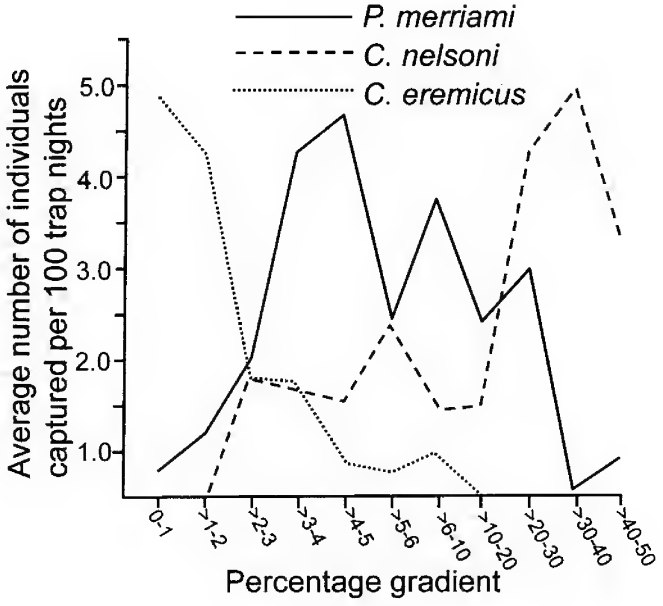

Figure 13. Abundance of three species of pocket mice compared with slope on the habitat plots.

Table 6. Characteristics of habitat plots having 3.7 or more understory plants per square meter.

Plot	Substrate	Slope (%)	Understory Plants per m^2	Percentage Composition			Individuals per 100 Trap Nights		
				Lechuguilla	Chino Grass	Fluff Grass	*P. merriami*	*C. nelsoni*	*C. eremicus*
74	Gravel	5	3.72	6	0	75	3.7	--	--
81	Cobbles	43	4.43	28	61	0	0.6	3.3	--
29	Boulders	40	5.28	23	12	0	--	3.3	--
13	Gravel	5	7.97	28	9	45	3.9	2.2	--
62	Gravel	26	9.04	31	9	18	5.4	0.6	--
82	Cobbles and Boulders	5	10.35	14	25	9	5.6	2.2	1.1
6	Gravel	4	13.35	13	0	47	2.3	--	0.9

nelsoni at Dugout Wells may be attributed either to the relative abundance of chino grass and lechuguilla or to population pressures which may have caused them to migrate from their normal habitat. Ten years after my study, Baccus (1971) found similar conditions at Dugout Wells.

The Chihuahuan pocket mouse (*C. eremicus*) was most abundant where the slope was <2% (Fig. 13). None were taken where the gradient was >9%. This species apparently does not favor steep slopes since none were collected on slopes containing fine powdery soils with fine gravels and sparse vegetation (Plot 69; Plate 13C-D) or slopes with soft sandy soils, sparse vegetation and larger rocks (Plot 40; Plate 15A-B), immediately adjacent to sandy loam flats containing high populations of Chihuahuan pocket mouse. That individuals of this species may occasionally venture onto steep slopes, however, is illustrated by one marked animal from the Eremicus plot which was trapped once on the bluffs surrounding the plot.

Distribution and Abundance of Pocket Mice in Relation to Soil Texture

Perognathus merriami.—Although this species was captured on all soil types (Fig. 14A) in the Big Bend area, it attains it peak of abundance on sandy loams, but was also common on the more compact soils containing a relatively high percentage of clay. For example, the soils of the Merriami plot were primarily sandy clay loam (Fig. 9). These clayish soils are tighter and less easily dug by rodents than the looser sandy loams.

Borell and Bryant (1942) trapped only four specimens of this rodent in Big Bend, from a sand flat near Mariscal Mountain. Although they trapped in many sandy areas, they were unable to catch other specimens. They concluded that tracts of hard rocky soil probably are probable barriers to the dispersal of *P. merriami*.

Denyes (1951) stated in her unpublished thesis that *P. merriami* is restricted to soft soils, though in the published account (1956) she recorded this mouse on both hard and soft soils. For example, she listed 20 individuals trapped on the gravelly and stony loams (Reeves series) of the Creosote-Ocotillo-Mesquite association, which is a greater number than she reported for any other association. She indicated that *P. merriami* was abundant in this association, although the soil was fairly hard.

Denyes (1954) showed experimentally that *P. merriami* can construct burrows in hard, dried clay loam soils by chewing its way through the hard outer crust. She believes that the reason *P. merriami* "are seldom taken on hard soils is probably a result of the opportunity to select more pliable soils in nearby habitats in relation to the balance between other factors which may be used as keys to selection." Baker (1956) apparently misinterpreted Denyes (1954) when he stated that she

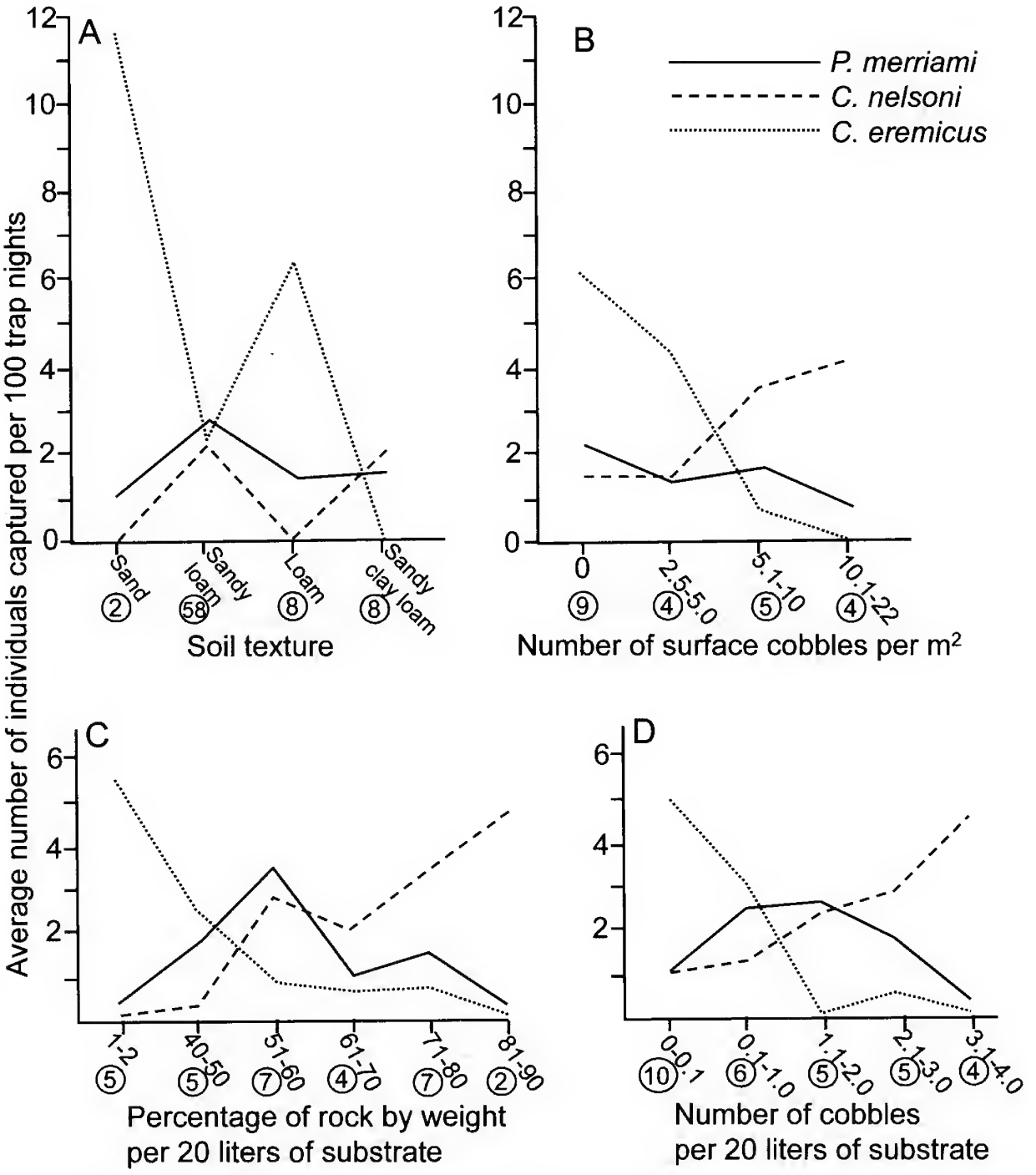

Figure 14. Abundance of three species of pocket mice compared with (A) soil texture, (B) average density of cobbles (rocks ranging in diameter from 7.5 to 40 cm) exposed on the surface, (C) percentage of rocks in the substrate, and (D) average number of cobbles per 20-liter substrate sample. Circled values indicate number of habitat plots sampled.

had shown experimentally that *P. merriami* is unable to make burrows in hard soils. Using the statements of Denyes (1954) and Borell and Bryant as evidence, Baker stated that heavy, rocky soils are barriers to the dispersal of this species in Coahuila, Mexico.

Results of my investigation reveal that the types of soil which Borell and Bryant (1942), Denyes (1951), and Baker (1956) indicated are barriers to the dispersal of this species are, in fact, its preferred types in the Big Bend area. Blair (1952) states that in southern Texas *P. merriami* shows no apparent preference for soil type and occurs in abundance on soils ranging from tight clays and caliche to deep sands. Baccus (1971) reported *P. merriami* in BBNP primarily from clay-loam soils, but also from sand.

Snap traps are ineffective in capturing *P. merriami*, which may account for the small numbers of the species captured by other investigators (Borell and Bryant 1942) in the Big Bend area. Although Denyes (1956) took specimens of *P. merriami* on nearly all types of soil, most individuals apparently were taken on silty clays and sandy loams. Baker (1956) believes that in Mexico this mouse probably occurs on alluvial soils bordering arroyos.

Chaetodipus nelsoni.—Nelson's pocket mice were not present on either deep sand or loam soils but were most abundant on shallow sandy loams and sandy clay loams (Fig. 14A). Denyes (1956) took them on loams, silt clay loams, fine sandy and silt limestones, clay loams and silt loams. Baker (1956) rarely collected *C. nelsoni* on sandy or other fine soils, and Borell and Bryant (1942) obtained no specimens from sandy washes. Baccus (1971) reported the species from sand, loam, and clay loam, when rocks and gravel were present.

Chaetodipus eremicus.—This mouse reached its peak of abundance on sands and loams and especially on the deep loams of the Rio Grande flood plain and the wide, dry, sandy washes of the arroyos running into the Rio Grande. Boeer and Schmidly (1977) found *C. eremicus* to be extremely abundant along the Rio Grande. Figure 14A indicates that *C. eremicus* reached its peak of abundance on sand. This, however, is a biased estimate because it represents the number of animals captured on a single plot. Denyes (1956) trapped *C. eremicus* in greatest numbers on loams, sandy loams and clay loams, and Baccus (1971) found the species in sandy soils.

Distribution and Abundance of Pocket Mice in Relation to Rock Content of the Substrate

As shown previously, the distribution and size of rocks in the soil are directly correlated with degree of slope. The distribution of pocket mice is better correlated with the number and size of rocks than with soil texture (Fig. 14B-D).

Merriam's pocket mouse is intermediate between *C. nelsoni* and *C. eremicus* in its preference for stony substrates (Fig. 14B-D; compare Plate 7C with Plates 6C and 8C). It was infrequently encountered on substrates containing either a large percentage of rocks (81-90%) or on those free of rocks. Although *P. merriami* reached its peak of abundance in substrates composed of 50-60% rocks, it was common on the coarse cobble outwashes (coarse gravelly foothills) extending from the canyons of the Chisos Mountains. Usually 500 or more boulders ≥40 cm in diameter per hectare were present in these areas (Fig. 15). Nelson's pocket mouse was equally abundant on these sites; the Chihuahuan pocket mouse was also present, but in smaller numbers (Fig. 16). Judd (1967), Baccus (1971), and Yancey et al. (2006) confirmed the occurrence of *P. merriami* in gravelly substrates in Big Bend. Wu et al. (1996) collected *P. merriami* from rock-free substrates in the Trans-Pecos, and reported a similar low density of *P. merriami* (<1 mouse per 100 trap nights) as I found (Figs. 14, 16) in rock-free habitats in Big Bend. The vegetation and substrate of Wu et al.'s (1996) study sites, while not its most preferred habitat, are well within the broad habitat tolerances of Merriam's pocket mouse as identified in this study.

Chaetodipus nelsoni reached its maximum abundance on substrates containing 80-90% rock (Fig. 14C; Plate 8C) with 3-5 cobbles per 20-liter sample (Fig. 14D) and 10-22 cobbles per square meter of surface area (Fig. 14B). On some sites, such as talus slopes (rough-broken mountain) and coarse gravelly outwashes, there were 5,000 or more boulders ≥40 cm in diameter per hectare (Fig. 15). Some boulders, especially on talus slopes, had diameters of ≥1.5 m (Fig. 15; Plate 16B).

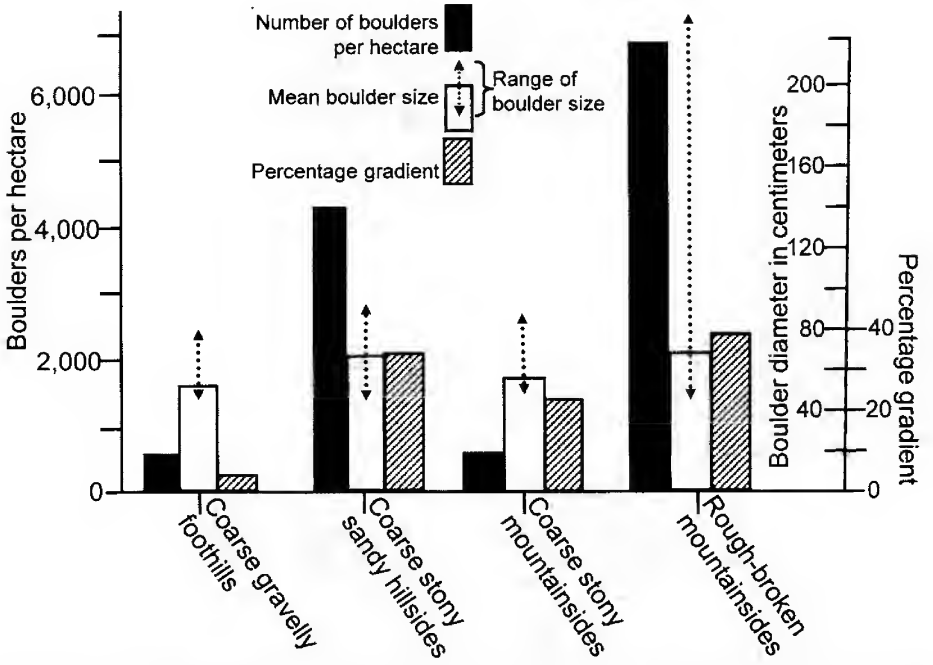

Figure 15. Density of boulders (≥40 cm in diameter), mean boulder size, and the percentage gradient compared with four habitat types in the Big Bend region.

The Chihuahuan pocket mouse reached its peak of abundance on deep soils free of rocks or nearly so (Fig. 14B-D; Plate 6A, C, E). It was noticeably less common where rocks comprised more than 50% (Fig. 14C) of the samples. Though less common, its range extended into the coarse rocky foothills (outwashes of the higher foothills) where loose sandy gravelly areas were interspersed with cobbles and small boulders (Fig. 16). On such sites all three species of pocket mice were occasionally encountered.

Distribution and Abundance of Pocket Mice in Relation to Vegetation Density

Features of the plant community which influence the distribution of pocket mice most are (1) proportion of understory plants to those in the overstory, (2) relative density and dominance of these plants in relation to the amount of bare ground and (3) general physiognomy of the plants, especially their height and their basal diameters.

Merriam's pocket mouse reached a peak of abundance in areas with a relatively sparse plant understory, 0.25-0.75 plants/m^2 (Fig. 17), and with at least 50% of the surface area free of plant cover (Merriami plot, Table 3; Plate 7). This species reached a second peak of abundance on some plots with high understory density. However, on plots with high populations of *P. merriami* and with 8-15 understory plants/m^2 (Fig. 17A), fluff grass was the most numerous plant. Apparently these short plants, each of which covers a relatively small surface area (Appendix II; Plates 3, 7), do not influence the distribution of this mouse as adversely as do taller plants with a similar density. Plots 74, 13, and 6 had a relatively dense understory composed largely of fluff grass (Table 6). All three plots had high populations of *P. merriami*. The large catch of *P. merriami* on Plot 62 (with a 26% gradient) was probably due to the predominance of small gravel in the soil (Plate 13B). In spite of the high relative density of lechuguilla and fluff grass, ground cover on this plot was sparse.

Nelson's pocket mouse attained a maximum density in areas where the understory was dense and the average plant height was 30-63 cm (lechuguilla and chino grass, respectively). In addition, understory plants outnumbered overstory plants nearly 18:1. On

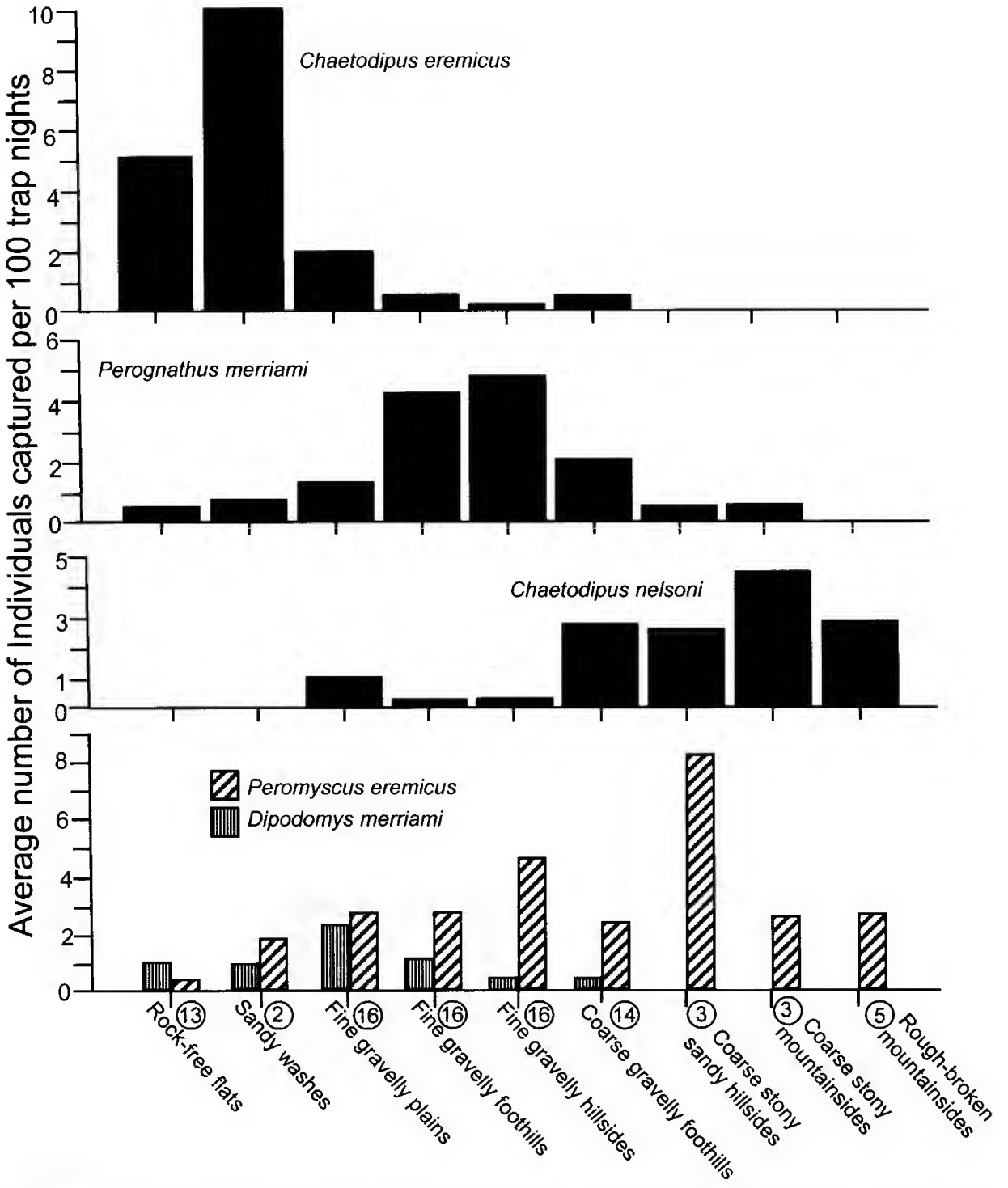

Figure 16. Average number (individuals per 100 trap nights) of five species of rodents captured on nine habitat types in the Big Bend area. Circled numbers are the number of plots represented in the sample.

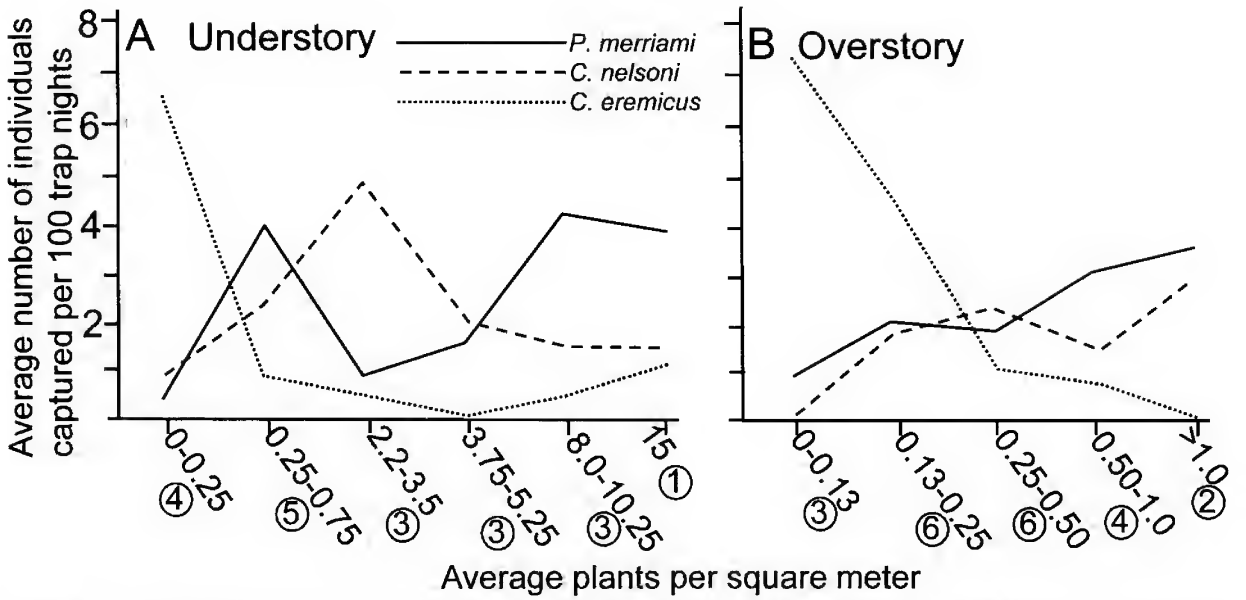

Figure 17. Abundance of pocket mice captured on the habitat plots compared with density of individual plants in the understory (A) and overstory (B). Circled numbers represent the number of plots sampled.

the habitat plots where the relative density of lechuguilla and chino grass was greatest (plots 81, 29, 82 and 13), populations of *C. nelsoni* were also high (Table 6).

The Chihuahuan pocket mouse reached its maximum abundance in habitat which had little ground cover (usually fewer than 0.25 understory plants/m^2; Fig. 17A) and extensive areas (usually much more than 50%) of bare ground. On the Eremicus plot, understory plants covered less than twice as much surface as the overstory. On most plots having an abundance of Chihuahuan pocket mice, the overstory appeared to cover more surface area at ground level than did the understory (Plate 11).

Distribution and Abundance of Pocket Mice in relation to Plant Species

There were fewer plant species on plots where large numbers of *C. eremicus* were captured than on those where captures were few. The reverse prevailed where Nelson's pocket mouse was abundant. Plots where Merriam's pocket mouse was taken assumed an intermediate position (see Figure 18 in Porter 1962). The physical aspects of the understory appear to exert a greater influence on the distribution of pocket mice than do those of the overstory.

In Porter (1962) I present a detailed analysis of the influence of selected plant species on pocket mouse distribution and how the various plants are used by pocket mice. Sotol, tasajillo, prickly pear, and tarbush were not strongly correlated with pocket mouse distribution. Other plant species were commonly found in areas favored by certain species of pocket mice, but it is probable that the distribution of pocket mice is influenced by the entire complex of vegetation, soil, slope, exposure and climate. There was an inverse or negative correlation between abundance of chino grass (Plate 15E) and that of Merriam's pocket mouse. The denser the stands of chino grass, the smaller was the population of *P. merriami*. Chihuahuan pocket mice seldom were present in chino grass areas, but *C. nelsoni* often reached maximum abundance in dense stands of this grass.

Lechuguilla (Plate 9) was present in the habitats of all three species of pocket mice, but in varying degrees of density and dominance. Populations of *C. nelsoni* frequently attained maximum density in heavy stands of lechuguilla if other habitat requirements were

suitable. Although lechuguilla apparently is a preferred understory plant for *C. nelsoni*, it is by no means a necessary one, since dense stands of chino grass or any species of plant with a similar physiognomy, such as false agave (*Hechtia texensis*) and wax plant (*Euphorbia antisyphilitica*), may serve as a substitute.

The Chihuahuan pocket mouse normally did not occur in dense stands of lechuguilla. However, it was abundant on Plot 24 which had a high relative density (45%) of lechuguilla, but there were only 0.18 understory plants/m^2 on this plot, 45% of which consisted of lechuguilla, mainly restricted to one edge of the plot, and 17% of leather plant. The overstory density was 0.43 plants/m^2, of which 45% were creosotebush. Hence, in the areas of the plot where *C. eremicus* was captured there were large areas of powdery, fine, gravelly sandy loam nearly devoid of ground cover. Adjacent to the plot was a dry wash and a slope leading to the wash containing boulders as large as 50-75 cm in diameter. The presence of the slope, the large rocks, and the lechuguilla probably accounted for the large number of *C. nelsoni* taken on this area of the plot. Lechuguilla was a common plant in most areas inhabited by *P. merriami*, but this mouse usually was not common where lechuguilla formed a dense ground cover.

Discussions and Comparisons of Habitat Preferences of Pocket Mice

Chaetodipus nelsoni.—Nelson's pocket mouse attained its peak of abundance on the steeper rocky slopes (30-40% gradient) containing sandy loam and sandy clay loam soils. The substrate, which was frequently shallow with numerous boulders and rock outcrops breaking through the surface, contained 80-90% rock. There were three to four cobbles per 20-liter sample and 10.8 to 21.5 cobbles per square meter of surface area. In areas of maximum abundance of *C. nelsoni* there were 500 to 14,300 or more boulders ≥40 cm in diameter per hectare (i.e., a maximum of nearly 1.5 boulders per m^2).

Ground cover in areas of maximum abundance of Nelson's pocket mouse usually was dense (well over 8 plants/m^2). Over 60% of the surface area usually was covered at ground level with vegetation. The major understory plants (lechuguilla and chino grass) in habitats preferred by *C. nelsoni* were usually 30-50 cm in height.

Habitats of *C. nelsoni* generally contained many more plant species than habitats where *C. eremicus* was abundant. The dominant understory plants were lechuguilla and chino grass. Overstory species were variable, but sotol and prickly pear generally were present. Steep slopes with sparse cover and fine gravel or with fine gravels and dense cover yielded small populations of Nelson's pocket mouse. This mouse was also common on steep slopes with large rocks and sparse cover. Thus rock size is probably of more importance in determining the abundance and distribution of Nelson's pocket mouse than slope or density of vegetation. *C. nelsoni* was not restricted to steep slopes; it occurred commonly on slopes with 3-6% gradient provided large rocks or dense vegetation, or both, were present. Nelson's pocket mouse was rarely found on the deep sandy loam and loam flats occupied by *C. eremicus*, but it was occasionally taken with *C. eremicus* on deep fine gravelly sandy loams (few cobbles, loose powdery soil) when vegetation consisted of sparse stands of lechuguilla.

Chaetodipus eremicus.—This species reached its greatest abundance on deep sandy loam or loam flats with less than 2% gradient, usually containing <1% rock by weight. *C. eremicus* was abundant in areas where the understory plants were sparse (frequently <0.25 plants/m^2), and the overstory vegetation was generally denser than the understory. Extensive areas of bare ground were exposed between the sparse clumps of vegetation, which usually covered less than 25% of the total surface area.

Habitats where *C. eremicus* was most abundant had fewer plant species than habitats preferred by the other two species. Short (≤12 cm) understory plants, such as ground cholla and fluff grass which clumped together so that considerable bare ground was exposed between clumps, apparently did not interfere with the distribution and abundance of this mouse. Although not restricted to any particular plant association, *C. eremicus* was most abundant in habitats containing creosotebush and mesquite.

The Chihuahuan pocket mouse was seldom found on steep slopes even though conditions of soil and vegetation appeared suitable. The combination of steep slopes (over 9% gradient), large rocks and dense vegetation appears to limit severely the distribution and abundance of this mouse. However, it was taken in small numbers in coarse rocky outwashes from the canyons of the Chisos Mountains in areas of ≥500 boulders per hectare. Yancey et al. (2006) found *C. eremicus* primarily on rock-free sandy soils in BBNP, though they reported the species occasionally in gravelly habitats.

Perognathus merriami.—This species reached its peak abundance on slopes with a gradient of about 5% having fine gravelly, sandy loam soils. Usually 50-60% of the substrate consisted of gravel with rocks seldom >7.5 cm in diameter. The sparse understory vegetation on preferred sites usually had 0.25-0.75 plants/m^2 if the ground cover were 25 cm or greater in height (lechuguilla) and as many as 7.4 or more plants/m^2 if the understory were less than 13-15 cm in height (fluff grass). This mouse attained its maximum abundance in habitats in which 50-60% of the total surface area was covered by vegetation at ground level.

The most frequent understory cover in preferred habitats was lechuguilla and fluff grass. The most frequent overstory plants were tarbush and mariola. These sites usually had more plant species than were found in habitats preferred by *C. eremicus*. Merriam's Pocket Mouse occurred uncommonly in habitats having sparse plant density (≤0.25 plants/m^2) and deep loam and sandy loam soils. At the other extreme, it was also uncommon on steep slopes where large rocks and dense (>2.2 plants/m^2), tall (at least 25 cm) vegetation were predominant. Steep slopes (10-30%) did not limit either the abundance or the geographic distribution of this mouse when soil and vegetation were suitable. For example, it was present in small numbers on steep slopes containing large rocks when the density of the vegetation was sparse and the soil deep.

Perognathus merriami had a wide range of habitat tolerance in the Big Bend area (Fig. 16), which seems to be typical in other parts of the range. Blair (1940) likewise noted that it occupied a wide range of habitat conditions in the Davis Mountains of western Texas, and in southern Texas. In the Panhandle of Texas, Blair (1954) observed a similarly large range of tolerance, and Judd (1967) indicates broad habitat preferences in Big Bend. The greater range of habitat tolerance displayed by *P. merriami* is illustrated by the following: (1) Each of the three species was taken exclusively on a roughly equivalent number of habitat plots (*P. merriami* exclusively on eight plots, and *C. eremicus* and *C. nelsoni* exclusively on 10 plots each). (2) *P. merriami* and *C. nelsoni* were captured together exclusively on 21 plots and *P. merriami* and *C. eremicus* were found together exclusively on 19 plots. (3) *C. nelsoni* and *C. eremicus* were taken together on only four plots. (4) All three species occurred together on nine plots. The information published by Denyes (1956) points to the same conclusion. She recorded *P. merriami* in many more plant associations in Brewster County, Texas, than either *C. nelsoni* or *C. eremicus*. Some *P. merriami* usually occurred in preferred habitats of each of the other two species. Baccus (1971) found *P. merriami* to be sympatric with both *Chaetodipus* species in BBNP, but found *C. nelsoni* and *C. eremicus* to be ecologically allopatric.

In the study area, the preferred habitat of *P. merriami* was intermediate between that of *C. nelsoni* and that of *C. eremicus* with respect to slope, density of vegetation and substrate characteristics (Figs. 13, 14, 16, 17). Because the Chihuahuan pocket mouse is better adapted to deep soft (powdery) sandy loam and loam soils and sparse understory vegetation, it is unable to compete successfully with *P. merriami* on the harder clayish soils where the understory vegetation is denser. Similarly, at the other extreme, *C. nelsoni* is unable to compete successfully with *P. merriami* in those intermediate areas because the understory vegetation is neither sufficiently tall nor dense and the soil lacks large rocks. Hence, these data indicate that *P. merriami* has occupied the intermediate habitat because it is better adapted than the other two species. Merriam's pocket mouse probably is crowded out of habitats preferred by the other two species by population pressures and because of its small size. Because *P. merriami* has a wide range of habitat tolerance it is able to occupy habitats not preferred by the other two species. In New Mexico, Bailey (1931) noted that although the habitat preferred by *P. merriami* was similar to that of *P. flavus*, *P. merriami* was more often found on stony or hard ground than in the mellow sandy valley bottoms occupied by *P. flavus*.

POCKET MOUSE HABITATS IN THE BIG BEND REGION

In previous sections it was shown that pocket mice in the Big Bend area have specific habitat preferences. Density and height of the understory, amount of surface area free of plant cover, size and density of rocks on the surface and below the surface of the soil, and distribution and spatial arrangement of surface rocks are among the most important factors influencing local distribution and abundance of pocket mice. Factors of lesser importance include gradient, soil texture, height and density of canopy vegetation, and species composition of the plant cover.

Neither the soil textural types nor the vegetation are sharply delineated in the area of study, but grade gradually from one type to another. The study area included nearly every conceivable combination of plant associates. Few if any rodents in the Big Bend area are restricted to any specific plant association or soil textural type, although they do attain their greatest abundance in those areas where characteristics of the habitat are optimum for survival.

Characteristics of the habitat in the Big Bend region differ from those in the desert areas of western Utah where Vest (1955) described several distinct biotic communities. There, Vest found several sharply delineated soil types and that each type supported a distinct complex of plant and animal associates. He also found that many species of plants and rodents were restricted almost entirely to a specific combination of soil and vegetation.

In the Big Bend area, however, where there is a gradation of soil types and plant associations, and where rodents are not restricted either to soil type or to plant associations, it was difficult to discern definite biotic communities. Hence, the study area was classified into more or less distinct *habitat types* for the purpose of comparing the habitat requirements of desert rodents. These are based chiefly on the characteristics of the substrate in relationship to the dominance of a particular species of pocket mouse, and to a lesser extent on slope, density and species composition of the vegetation, and other architectural characteristics of the habitat. Since plant associations seemingly are of lesser importance in the distribution of pocket mice, each habitat type discussed below may include one or more of the plant associations described by Thompson (1953), Tasmitt (1954) and Denyes (1956).

In estimating populations of Nelson's pocket mouse and Merriam's kangaroo rat (*Dipodomys merriami*), captures for every month were utilized, but, because of winter periods of inactivity of *P. merriami* and *C. eremicus*, capture records for the months of November through January were omitted from the calculations for these two species. Only the capture records from November through June were used in calculating population densities of the cactus mouse (*Peromyscus eremicus*).

Rock-free Flats (Plate 6A, C, E; Plate 11)

Altitude and Location.—550-850 m. (1) Rio Grande flood plains (Plate 11B, Plot 78), (2) flood plains of the Tornillo Creek, (Plate 11C, Plot 71), and (3) sandy loam flats below, and derived from, igneous volcanic capped sandstone cliff near upper Tornillo Flat (Plate 6A, C, E, Eremicus plot), and the lower portion of Tornillo Creek near the bridge (Plate 11A, Plot 77), in the area of San Vicente, and other localities.

Plots.—16, 32, 34, 35, 39, 41, 71, 77, 78, 93, 100, Eremicus plot.

Gradient.—Average, 1%; range, 0% on Rio Grande flood plain to 2.5% (Fig. 18A).

Substrate.—Deep loam, containing a high percentage of silt in the flats of the Rio Grande and Tornillo Creek flood plains; deep sandy loam below sandstone cliffs. It is a soft, powdery, pliable, easily dug soil that frequently develops a rather hard surface crust. Average percentage composition of soil for six plots: sand, 38; silt, 41; clay, 21. No surface or soil gravel was present in the deep loams near the Rio Grande and Tornillo Creek. Less than 1% of the substrate material by weight consisted of gravel in the steeper sandy loam areas, where rocks >2.5 cm were rare (Fig. 19; Plate 6A, C).

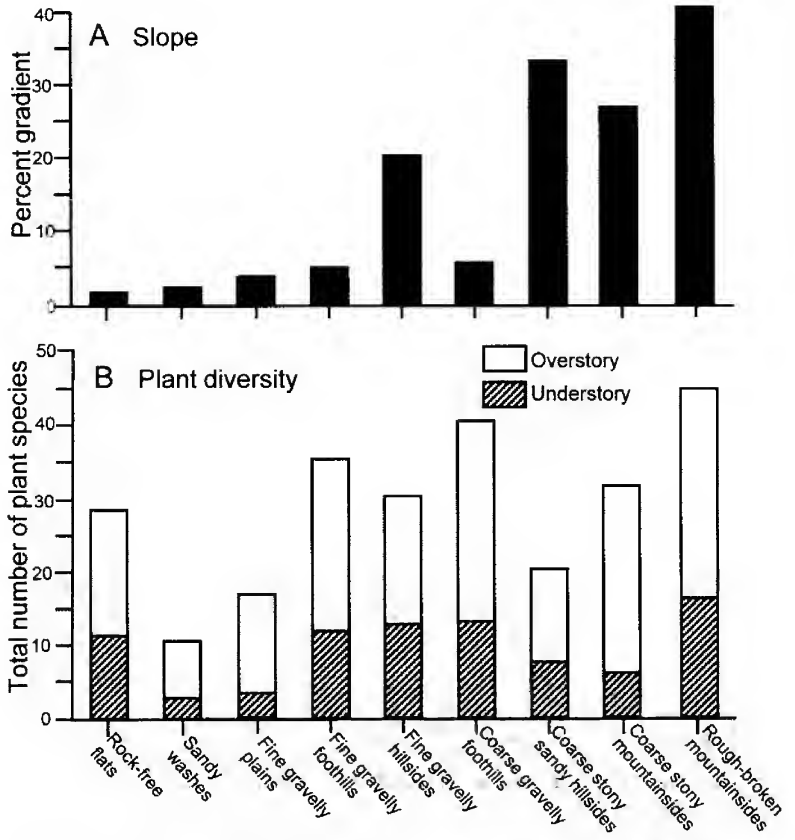

Figure 18. A. Average percentage gradient of several habitat types in the Big Bend region. B. The total number of plant species recorded on each of several habitat types in the Big Bend region. Data are derived from the habitat plots.

Density of Vegetation.—Generally sparse with <0.5 perennial plants/m^2. Overstory usually more dense than understory, but with <0.25 plants/m^2 (Plates 6A, E; 11). Understory usually has <0.13 plants/m^2 (Fig. 20).

Plant Species Composition.—Mean percentage plant species composition for all six plots studied is given in Appendix III. In the deep loams of the Rio Grande flood plains (plots 35, 71, and 78), mesquite, in the form of large clumps (up to 9 m or more in crown diameter) was the predominant plant (Plate 11B-C). These clumps were surrounded by extensive areas of bare ground. The understory plants were so sparse on plots 71 (Plate 11C) and 35, for example, that it was impractical to measure or record them. Plots located on sandy loam (32, 77, and the Eremicus plot) contained principally creosotebush (Plate 12B). Eleven understory and 17 overstory species were recorded on these plots (Fig. 18B; Appendix III).

Reptilian Associates.—The Common Side-blotched Lizard (*Uta stansburiana*) and the Marbled Whiptail (*Aspidoscelis marmorata*) were the most abundant reptiles in this habitat where *Uta* attained its maximum abundance. The Greater Earless Lizard (*Cophosaurus texanus*) was present, and the Desert Spiny Lizard (*Sceloporus magister)* was found on the loamy soils of the Rio Grande flood plains. A rattlesnake (*Crotalus*) was recorded on the Eremicus plot.

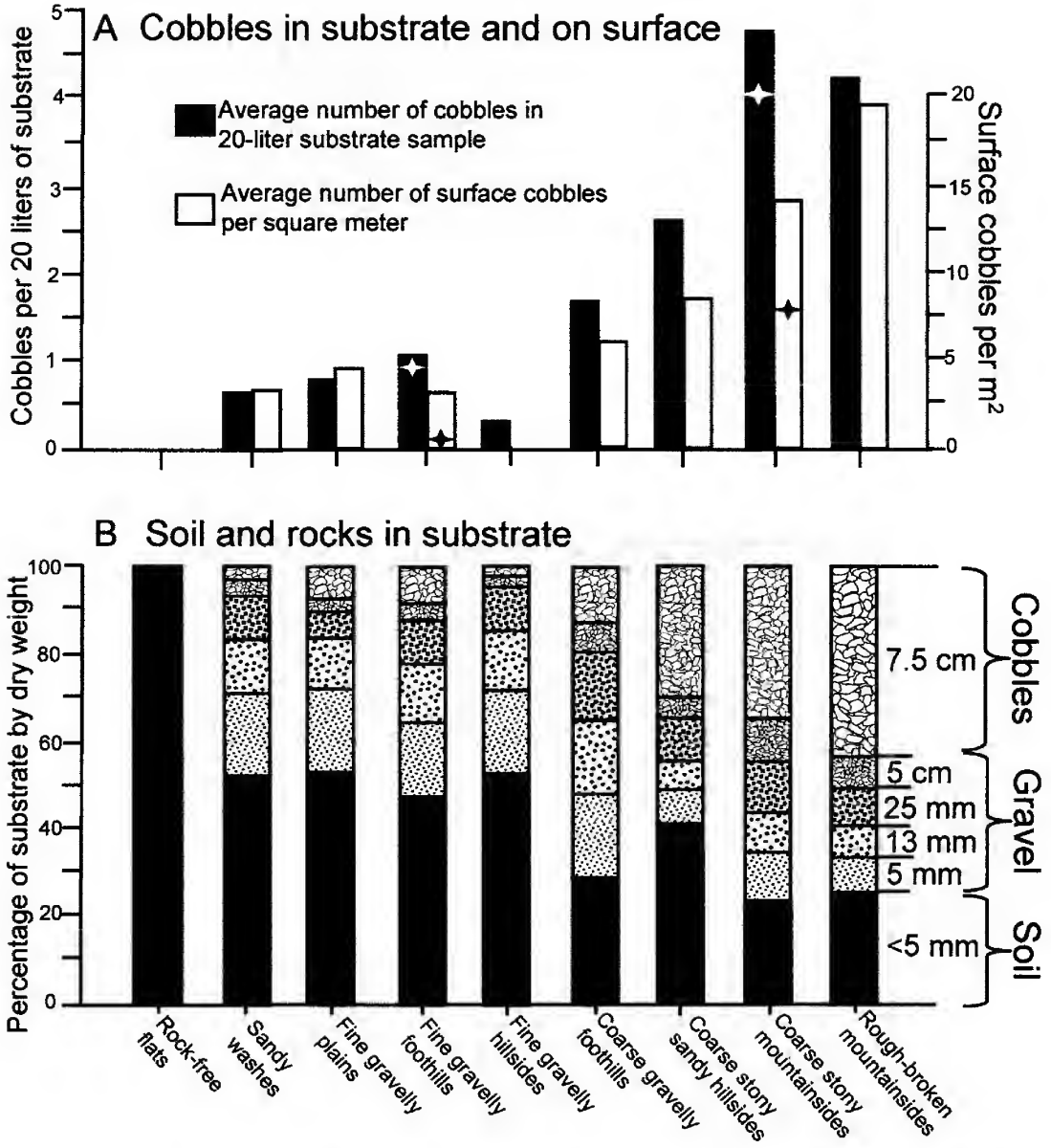

Figure 19. Soil and rock composition of nine habitat types in the Big Bend region based on the habitat plots. Cobbles as defined in this study include rocks 7.5-40 cm in diameter. A. Average number of cobbles per square meter of surface area, and in a 20-liter sample of substrate. Stars in the fine gravelly foothills and the coarse stony mountainside represent cobbles in the Merriami plot, and the Nelsoni plot, respectively. The Eremicus plot is a rock-free flats habitat containing no cobbles. B. Percentage of the total average dry weight of soil and assorted sizes of rocks in a 20-liter substrate sample. Minimum diameter of each size class is shown to the right.

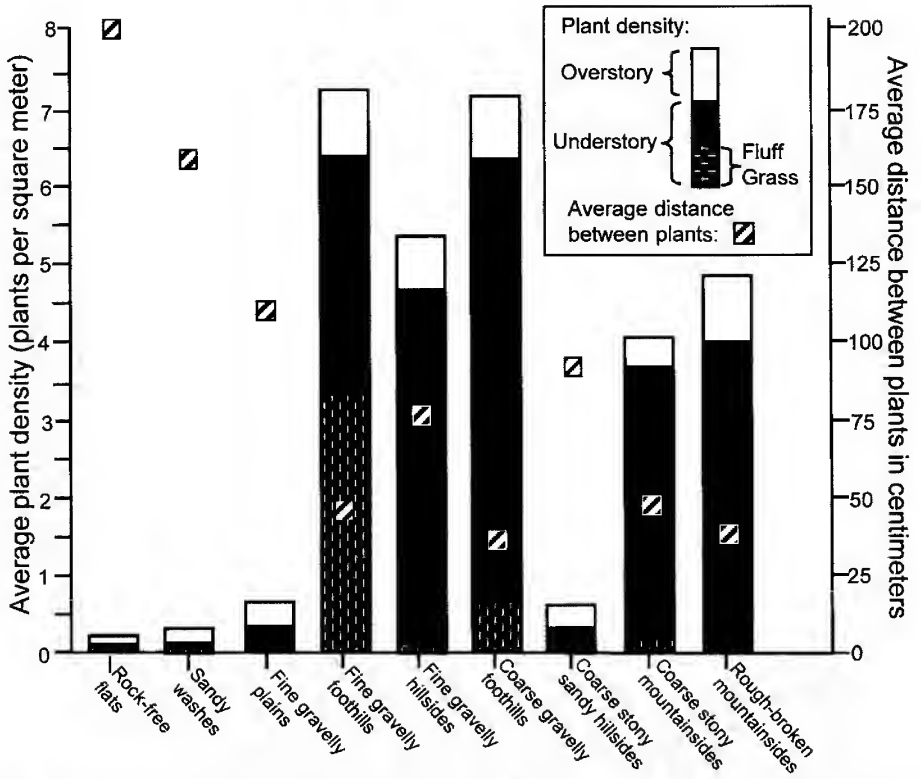

Figure 20. Plant density on nine habitat types in the Big Bend area. Stippled area indicates the mean proportion of fluff grass (which contributes very little to ground cover) in the understory.

Rodent Associates.—The predominant rodent in this habitat was the Chihuahuan pocket mouse (Fig. 16). Merriam's kangaroo rat (*Dipodomys merriami*) was next in abundance, especially on sandy loam soils. Kangaroo rats were not common on the deep alluvial soils adjacent to the Rio Grande. Merriam's pocket mouse and the cactus mouse were uncommon and *C. nelsoni* was absent. The spotted ground squirrel (*Xerospermophilus spilosoma*), the Texas antelope squirrel (*Ammospermophilus interpres*), and southern plains woodrat (*Neotoma micropus*) were present in small numbers.

Remarks.—On the Eremicus plot, *P. merriami* utilized holes in the sandstone outcroppings surrounding the plot. Nelson's pocket mouse was not trapped in this habitat type, although one individual was taken about 6 m up on a ledge of the sandstone butte surrounding the Eremicus plot (Fig. 8; Plate 6). This butte was entirely surrounded by habitat preferred by *C. eremicus*. The paucity of the cactus mouse in this habitat is likely a reflection of the sparseness of the vegetation and its accompanying lack of nesting sites. Lechuguilla and sotol seem to be important as nesting sites of this mouse.

Sandy Washes and Arroyos (Plate 10)

Altitude and Location.—Most frequent at lower elevations (600 m) but some sandy washes occur in the foothills at elevations of 1,100-1,300 m.

Plots.—36, 76, 95.

Gradient.—2% or less (Fig. 18A).

Substrate.—Sand, loamy sand, and sandy loam. Average percentage composition of soil on three plots:

sand, 80; silt 10; clay, 10. Sandy washes in the foothill areas have deep, fine textured, moderately permeable, brown gravelly soils which sometimes occupy depressional drain areas within the Pinal and other soil series and develop over gravelly outwash materials from the Chisos Mountains. Gravels frequently were present in the central portion of the wash where the main intermittent stream flow occurred. In these areas, gravel constituted as much as 50% of the total weight of the substrate material (Fig. 19B). Some cobbles were present in these sections (Fig. 19A), and vegetation was sometimes completely absent. On each side of the central gravelly section were deep sandy overflow areas.

Density of Vegetation.—Density of the vegetation in this habitat type was similar to that of the rock-free flats in its sparseness (Fig. 20). The overstory was also denser than the understory. Sandy washes usually had little if any cover at ground level.

Plant Species Composition.—Considerable variation was found in the plant species on sandy washes. In areas near mountains, species characteristic of mountains may predominate. The vegetation was analyzed only at one plot (76; Plate 10) near the Rio Grande. Plant cover on this plot consisted mainly of *Porophyllum scoparium*, huisache (*Acacia minuata*), creosotebush, and tasajillo. But this is not representative because huisache is very uncommon in the general area. The most abundant understory plants were sand dropseed (*Sporobolus cryptandrus*) and fluff grass (Appendix III.).

Reptilian Associates.—The Marbled Whiptail was observed in this habitat.

Rodent Associates.—*Chaetodipus eremicus* was the most abundant rodent. Merriam's pocket mouse was uncommon and Nelson's pocket mouse absent. Merriam's kangaroo rat and the cactus mouse were both present in small numbers (Fig. 16).

Fine Gravelly Plains (Plate 12)

Altitude and Location.—Widespread, covering many square kilometers of desert lowlands from the flood plains (600 m) to the foothills (1,000 m).

Plots.—8, 9, 10, 14, 22, 23, 24, 25, 26, 45, 46, 63, 64, 65, 66, 68, 101.

Gradient.—Average, 3%; range, 2-10% (Fig. 18A).

Substrate.—Powdery sandy loam, relatively soft, pliable, and easily dug by rodents. Average percentage composition of soil samples on nine plots: sand, 65; silt, 22; clay, 12. Approximately 50% of the substrate was rock with a relatively small proportion of cobbles (Fig. 19; Plate 12E, Plot 101).

Density of Vegetation.—Plant cover of this habitat was slightly denser (>0.75 plants/m^2) than on sandy washes (Fig. 20; Plate 12A). On average, understory plants were slightly denser than overstory. Both the overstory and the understory of this habitat usually have >0.25 plants/m^2.

Plant Species Composition.—The overstory (Appendix III) was principally creosotebush (Plate 12B). In some areas, leather plant was common; in others it was absent. The understory was principally lechuguilla (Plate 9; Appendix III). Lechuguilla (Plate 9) and chino grass (Plate 15E) may be present, and the strawberry pitaya (*Echinocereus stramineus*; Plate 12C) frequently occurs in these areas. Only 4 understory and 13 overstory species were recorded in this habitat type (Appendix III; Fig. 18B).

Reptilian Associates.—Marbled Whiptails and Common Side-blotched Lizards occurred in this habitat in small numbers.

Rodent Associates.—The cactus mouse occurred in this habitat and the kangaroo rat (*Dipodomys merriami*) reached its maximum abundance here (Fig. 16; Plate 12D). All three species of pocket mice were present, with *C. eremicus* the most abundant and *C. nelsoni* the least. Woodrats (*Neotoma*) and spotted ground squirrels occurred in small numbers.

Remarks.—The deep pliable soil and sparse understory enable *C. eremicus* to compete successfully with *P. merriami* in this habitat and the absence of large rocks, coupled with a sparse plant understory, allows it to compete successfully with *C. nelsoni*.

Fine Gravelly Foothills (Plate 7)

Altitude and Location.—About 1,100 m elevation in the region of Lone Mountain and in some areas along the base of the Chisos Mountains. It was usually sandwiched between the canyon outwashes and the fine gravelly plains. In areas where fine gravelly foothills were absent, the fine gravelly plains habitat joined directly either with the coarse gravelly foothills, with the coarse stony mountainsides, or with the rough-broken mountainsides habitats.

Plots.—6, 11, 12, 13, 44, 49, 57, 58, 59, 60, 73, 74, Merriami plot.

Gradient.—Average for 14 plots, 5%; range 3-8% (Fig 18A).

Substrate.—Soil in this habitat contained more clay than the fine gravelly plains habitat; consequently, it was more compact. It ranged from clay loam to sandy clay loam and sandy loam. Average percentage composition of four plots: sand, 61; silt, 19; clay, 20. Except for a slightly higher percentage of rocks (Fig. 19) 2.5 cm or larger, the gradation of rocks in this habitat (Plate 7C) was similar to that of the fine gravelly plains (Plate 12E, Plot 101).

Density of Vegetation.—The understory density ranged from 0.85 to 13.35 plants/m^2 (Tables 2, 6), with an average of almost 6.5 plants/m^2 (Fig. 20). The high average density of the understory was due in part to a high proportion of fluff grass (Fig. 20; Tables 4, 6; Appendix III), which as noted previously, covers relatively little surface area (Appendix II).

Plant Species Composition.—This habitat had a larger number of plant species than usually occurred in the fine gravelly plains habitat (Fig. 18B). Tarbush and mariola were the two most abundant shrubs recorded here (Appendix III). Fluff grass, lechuguilla, and black grama (*Bouteloua eriopoda*) were the most abundant understory species.

Reptilian Associates.—The Marbled Whiptail was the most abundant reptile (28 were caught in live traps). Other lizards included *Aspidoscelis exsanguis*, *A. inornata* and *Uta stansburiana.*

Rodent Associates.—Merriam's pocket mouse not only acquired its greatest abundance in this habitat, but it also was the most abundant rodent. Nelson's and Chihuahuan pocket mice were present in small numbers (Fig. 16). *P. merriami* was common in the coarse gravelly foothills, but much less so on the fine gravelly plains (Fig. 16). Presumably because of the paucity of large rocks and the absence of a tall, dense understory, *C. nelsoni* was uncommon except where this habitat intergraded with the coarse gravelly foothills. In this transition zone there were occasional areas of large rocks which were preferred by *C. nelsoni*. Because of the harder clayish soils and the denser understory vegetation of the fine gravelly foothills, populations of *C. eremicus* were low in this habitat. *C. nelsoni* was the least common pocket mouse probably because of the relative sparseness of the vegetation in this habitat type compared with that usually inhabited by *C. nelsoni*. Hence the lessened competition between *P. merriami* and the other two species of pocket mice undoubtedly accounts for the almost exclusive presence of *P. merriami* in this habitat.

The cactus mouse was abundant in this habitat. White-throated woodrats (*Neotoma albigula*; Plate 14C), spotted ground squirrels, and Texas antelope squirrels were also present. The presence of lechuguilla and sotol may account for the abundance of cactus mice in this habitat.

Remarks.—This habitat differs from the fine gravelly plains in its more compact soil, and its denser and more diverse vegetation, particularly in the understory (Figs. 18B, 20). However the denser understory in the fine gravelly foothills does not result in extensive ground cover because of the preponderance of fluff grass. Note the small clumps of fluff grass visible in open areas of the fine gravelly foothills (Plate 7A-B), which are absent in the fine gravely plains (Plate 12A). Although the Merriami plot had a high proportion of fluff grass, other plots representing this habitat had even higher densities of fluff grass, resulting in a very large mean understory density for the fine gravelly foothills (Fig. 20).

Fine Gravelly Hillsides (Plate 13)

Altitude and Location.—Distributed uncommonly throughout the study area at elevations of 600-1,100 m.

Plots.—1, 31, 62, 69, 94.

Gradient.—Average for four plots, 20%; range, 14-26% (Fig. 18A).

Substrate.—The soil on two plots was sandy loam; on a third, sandy clay loam (approaching sandy loam); on a fourth, sandy loam (approaching sandy clay loam). Average percentage composition of the soil on four plots: sand, 65; silt, 18; clay, 17. The gravel was similar to that of the fine gravelly plains and fine gravelly foothills (Fig. 19; Plate 13B, D).

Density of Vegetation.—Of two plots sampled for vegetation in this habitat type, Plot 69 was similar (Plate 13C, overstory 0.15 plants/m^2, understory 0.52 plants/m^2) to that of the gravelly plains habitat (Plate 12), whereas Plot 62 (Plate 13A, overstory, 1.47 plants/m^2 and understory, 9.04 plants/m^2) was much denser and similar to the vegetation on the coarse stony mountainside habitat.

Plant Species Composition.—There was considerable variation in the plant cover in this habitat type. Plot 62 was near the foothills and had vegetation consisting of components from both the coarse stony hillside habitat (such as sotol, 13%; chino grass, 9%; *Dalea formosa*, 14%; and *Acacia angustissima* var. *texensis*, 9%) and the fine gravelly foothill habitat (such as *Gutierrezia*, 18%; *Dasyochloa pulchella*, 19%; and *Gymnosperma*, 16%; Appendix III).

The overstory vegetation on the second plot (69) was chiefly creosotebush and mesquite, which were the principal components of the fine gravelly plains and the rock-free flats. Purple-tinged prickly pear (*Opuntia macrocentra*; Plate 14D) and tasajillo (Plate 15D) were present. The understory vegetation was sparse and consisted of false grama (*Cathestecum erectum*), 38%; drop seed (*Sporobolus wrightii*), 20%; and *Bouteloua trifida*, 11%.

Reptilian Associates.—The Collard Lizard (*Crotaphytus collaris*) and Marbled Whiptail were present. A Long-nosed Snake (*Rhinocheilus lecontei*) was taken from a trap on Plot 62.

Rodent Associates.—Merriam's pocket mouse and the cactus mouse were the two most abundant rodents in this habitat (Fig. 16). One *C. eremicus* was trapped in a wash cutting through the hill on Plot 94, and two Merriam's kangaroo rats were taken on a small road-like terrace which wound up the hill from the flat below. Only three specimens of *C. nelsoni* and two species of ground squirrels (*Ammospermophilus interpres* and *Xerospermophilus spilosoma*) were taken in this habitat.

Remarks.—The abundance of Merriam's pocket mice in this habitat indicates that slope alone does not adversely influence the distribution and abundance of this mouse. The fact that Plot 62 had a rather dense plant understory (Table 6; Plate 13A) would indicate that the absence of large rocks on this plot and the presence of deeper soils were the major reasons for the abundance of Merriam's pocket mouse and the uncommon occurrence of *C. nelsoni*. The absence of large rocks on Plot 69 (Plate 13D) undoubtedly accounts for the paucity of *C. nelsoni*. Hence, it is probable that the *apparent* preference of *C. nelsoni* for steep slopes (Fig. 13) is associated with the usual occurrence of large rocks and dense understory vegetation on steep slopes (Fig. 12), rather than with the degree of the slope *per se*. Data indicate that these two factors were also responsible for the usual paucity of *P. merriami* on steep slopes. The absence of *C. eremicus* on these slopes despite the absence of large rocks, the sparseness of the vegetation and the presence of a "pliable" soil (Plot 69), suggests that slope alone may restrict its distribution and abundance.

Coarse Gravelly Foothills and Outwashes (Plate 14)

Altitude and Location.—Around the base of the Chisos Mountains (1,000-1,700 m). In some places it extended from the mouths of the canyons onto fine gravelly foothills and fine gravelly plains. In these localities the major intermittent streams had cut below

the main level of the wash, leaving adjacent secondary overflow areas or low terraces on which large rocks had been deposited. These course gravelly washes gradually graded into sandy washes.

Plots.—2, 3, 4, 5, 7, 38, 47, 48, 50, 51, 53, 54, 56, 82.

Gradient.—Average for 14 plots, 5%; range, 3-7% (Fig. 18A).

Substrate.—Sandy loam (approaching loamy sand), and sandy clay loam. Average percentage composition of samples: sand, 68; silt, 19; clay, 13, similar to the texture of fine gravelly plains. The coarse gravelly foothills had a high percentage of rocks, a relatively high average number of cobbles per 20-liter sample, and an average of 5.4 surface cobbles per square meter (Fig. 19A). There were about 430 boulders (≥ 40 cm) per hectare (Plot 82). Average diameter of boulders was 46 cm; the largest was 84 cm (Fig. 15; Plate 14E).

Density of Vegetation.—Recorded density of the understory in this habitat is not a valid indication of the amount of surface area covered because many of the plants were species which cover very little surface area at ground level as compared to lechuguilla and chino grass. This habitat had a denser overstory than other habitats (Fig. 20).

Plant Species Composition.—This habitat had a large variety of species of overstory and understory plants (Fig. 18B). Grasses (13 species) made up the bulk of the understory (Appendix III); lechuguilla and chino grass were not abundant. The overstory, likewise, was composed of a great variety of species of shrubs many of which were dominants in other habitats. Because of the great variety of species, it was difficult to designate any one or two species as dominants in the understory or the overstory. In the mouth of Pine Canyon, this habitat type was composed chiefly of bear grass (*Nolina erumpens*), grama grasses (*Bouteloua*), lechuguilla and sotol.

Reptilian Associates.—The following lizards and snakes were recorded in this habitat: *Coleonyx variegatus, Crotaphytus collaris, Cophosaurus texanus, Sceloporus poinsettii, Phrynosoma modestum, Aspidoscelis marmorata, A. exsanguis, Diadophis punctatus regalis, Masticophis flagellum, M. taeniatus, Salvadora grahamiae, Arizona elegans, Pituophis catenifer, Lampropeltis getula, Hypsiglena torquata, Crotalus molossus, C. lepidus* and *C. scutulatus.*

Rodent Associates.—Merriam's and Nelson's pocket mice were about equally abundant (Fig. 16). The Chihuahuan pocket mouse was only about 25% as abundant as the other two, and it was taken on only 5 of the 14 plots. White throated woodrats (Plate 14C) and cactus mice (Plate 15C) were both common in this habitat, in which the former probably attains its peak of abundance in this region. *Dipodomys merriami* (Plate 12D) and two species of ground squirrel (*X. spilosoma* and *A. interpres*) were also present.

Remarks.—This habitat had a greater diversity of reptiles and mammals than any of the others. Four of the 14 plots trapped in this habitat yielded all three species of pocket mice. The soil and gravel characteristics (Fig. 19; Plate 14E) were intermediate between those of the coarse stony mountainside (Plate 8C) and the fine gravelly foothills (Plate 7C). It was frequently characterized by alternating areas of coarse and fine gravels (see Plate 14B), and by intermediate characteristics of the vegetation. When this situation prevailed, *C. nelsoni* was usually found in the areas of cobbles and coarse gravel whereas *P. merriami* was more inclined to occur in the fine gravels. A few shallow sandy washes and the accompanying sparse vegetation probably accounted for the presence of *C. eremicus* on some of the plots. Sotol, Torrey's yucca and prickly pear provided nesting sites for the white-throated woodrat and cactus mouse.

Coarse Stony Sandy Hillsides (Plate 15)

These hillsides were derived from sandstone hills with igneous volcanic caps. The surface is covered with rock fragments which have weathered from the igneous cap.

Altitude and Location.—At sites throughout the area 850-1,100 m: upper Tornillo Flat Lower Tornillo bridge, near Glenn Spring, Glenn Spring Road, 12.7 km west of Panther Junction on the Basin Junction-Maverick Junction Highway.

Plots.—30, 40, 67.

Gradient.—Average of three plots, 33%; range, 21-47% (Fig. 18A).

Substrate.—Soil material was calcareous, ranging from sandy loam (approaching loamy sand) to sandy clay loam; deep soft and not forming a hard-baked crust, hence easily dug by pocket mice. Average percentage composition of three plots: sand, 66; silt, 19; clay 15. Over 65% of the substrate material sampled in this habitat type was rocks, of which over 30% by weight was cobbles (Fig. 19B). There were >2.5 cobbles per 20-liter sample, and >8 cobbles per square meter of surface area (Fig. 19A). Over 4,200 boulders were recorded per hectare on Plot 40 (Fig. 15; Plate 15B), for an average of one boulder per 2.4 m^2. The average boulder was 66 cm in longest dimension; the largest recorded was 107 cm.

Density of Vegetation.—One feature of this habitat was the sparsity of vegetation (Fig. 20; Plate 15A). In this respect it was similar to the fine gravelly plains habitat.

Plant Species Composition.—This and the fine gravelly hillside habitat (Plot 69) were the only steep slopes on which creosotebush was noted. Creosotebush (Plate 12B) and chino grass (Plate 15E) were the most abundant overstory and understory plants, respectively, in this habitat (Appendix III). Ocotillo (*Fouquieria splendens*), narrow leafed moonpod (*Selinocarpus angustifolius*), and false grama were present. Tasajillo (Plate 15D) reached its maximum abundance in this habitat.

Reptilian Associates.—The Greater Earless Lizard was observed in this habitat.

Rodent Associates.—Only three species of rodents were taken in this habitat: *C. nelsoni*, *P. merriami* and *Peromyscus eremicus*. Nelson's pocket mouse was nearly five times as abundant as *P. merriami* (Fig. 16), and the cactus mouse (Plate 15C) reached its peak abundance here. Kangaroo rats were absent from this habitat and others with an abundance of large rocks (Figs. 16, 19), as is typical of bipedal heteromyids (Brown and Harney (1993).

Remarks.—The presence of cobbles and boulders undoubtedly accounted for the common occurrence of *C. nelsoni*, despite the sparseness of the understory. This indicates that a dense overstory is not necessary for *C. nelsoni* if large rocks are present. It was shown previously that slope does not limit the distribution or abundance of *P. merriami* when large rocks are absent and the soil deep. The presence of small numbers of *P. merriami* in this habitat suggests that large rocks do not restrict its distribution if the understory vegetation is sparse and the soil deep, but they may influence its abundance, at least when in competition with *C. nelsoni*.

Coarse Stony Mountainsides (Plate 8)

Altitude and Location.—Along the base of the Chisos Mountains (1,000 m) where rocky outcrops predominate without extensive cliffs. It is present along the base of Nugent Mountain (Nelsoni plot, Plate 8) and near the Glenn Spring and Pine Canyon roads.

Plots.—27, 81, Nelsoni plot.

Gradient.—Average of three plots, 26%; range, 15-43% (Fig. 18A).

Substrate.—Loamy sand, sandy and silt loam. Average percentage composition: sand, 64; silt, 26; clay, 10. Fine gravels and stony materials 15-75 cm deep overlie thin-bedded, igneous parental material. The nature of the rocks is shown in Plate 8C and Figures 15 and 19. Rocks comprised nearly 80% by weight of the substrate. There was a greater number of cobbles in this habitat than in any other (Fig. 19A). The larger rocks were fragments of the outcropping of igneous parental material, and usually they were long thin fragments (Plate 8C). There were on average, about 500 boulders per hectare in this habitat type (Fig. 15), for an average of one boulder for every 20 m^2. The average longest boulder diameter was 56 cm; the largest, 94 cm.

Density of Vegetation.—The overstory of this habitat was not much denser than that of the rock-free flats and fine gravelly plains, but the understory vegetation was much denser (Fig. 20). A comparison of the percentage of surface area covered by understory

plants in this habitat with that of the fine gravelly foothills (compare the Nelsoni plot with the Merriami plot, Appendix II), and the coarse gravelly foothills indicates that more of the surface area of the coarse stony mountainside was covered at ground level with vegetation. The main reason for this is that fluff grass in the fine and coarse gravelly foothills covered less surface area than did chino grass and lechuguilla in the coarse stony mountainsides.

Plant Species Composition.—The principal overstory plants were leather plant, prickly pear (three species, Appendix III), ceniza, Parry's ruellia (*Ruellia parryi*), and sotol. The dominant understory species were chino grass and lechuguilla (Appendix III) which formed a dense understory 25-50 cm high.

Reptilian Associates.—*Aspidoscelis marmorata*, *A. exsanguis*, *Eumeces obsoletus*, *Diadophis punctatus regalis*, *Crotalus molossus* and *C. scutulatus* were observed in this habitat.

Rodent Associates.—*Chaetodipus nelsoni* and the cactus mouse were the most abundant rodents (Fig. 16). *P. merriami* was not common. Only one white-throated woodrat was captured even though the nests of this species were fairly common under dead sotols.

Remarks.—Merriam's kangaroo rat and adult *C. eremicus* were not recorded in this habitat (Fig. 16). One juvenile *C. eremicus* was collected. Apparently steep slopes, large rocks, and dense vegetation were factors which prevented *C. eremicus* from occupying coarse stony mountainside. Probably the dense, tall understory vegetation (chino grass and lechuguilla) and the cobbles and boulders were the principal factors limiting the number of *P. merriami*. The abundance of cactus mice may be related to the presence of lechuguilla and sotol.

Rough-broken Mountainsides (Plate 16)

Altitude and Location.—Characterized by large cliffs and boulder strewn talus slopes, at elevations ranging from 600 m (Rio Grande) to 1,370 m (foothills of the Chisos Mountains). Numerous mountainous areas in the Big Bend region have this type of habitat. Some are of limestone origin (Dead Horse Mountains); others are igneous (Grapevine Hills, Chilicotal Mountain, and Burro Mesa).

Plots.—21, 28, 29, 61, 70, 75.

Gradient.—Average six plots, 39%; range 21-60% (Fig. 18A).

Substrate.—Sandy loam sandy clay loam (approaching clay loam), loam. Average composition of soil samples: sand 56; silt, 19; clay, 25. Nearly 80% by weight of the substrate in this habitat was rock (Fig. 19B). There were more than four cobbles per 20-liter sample (Fig. 19A) and more than 6,700 boulders per hectare (i.e., one boulder per 1.5 m^2; Fig. 15). The average boulder was 66 cm in the greatest dimension; the largest, 229 cm (Fig. 15; Plate 16B)

Density of Vegetation.—A dense understory was characteristic of this habitat (Fig. 20). More than 3.9 plants/m^2 were recorded in the understory; 0.7 in the overstory.

Plant Species Composition.—A greater variety of plant species was found in this habitat than in any of the other habitats studied (Fig. 18B; Appendix III). It was difficult to designate a dominant overstory plant because several species were equally abundant, particularly *Ruellia parryi*, *Carlowrightia linearifolia*, and *Ephedra* (Appendix III). The dominant species of the understory were chino grass and lechuguilla. False grama and cotton top (*Digitaria californica)* were common on some plots but not on others.

Reptilian Associates.—The following squamates were observed in this habitat: *Eumeces obsoletus*, *Crotaphytus collaris*, *Sceloporus merriami*, and *Crotalus molossus*.

Rodent Associates.—*Chaetodipus nelsoni* and the cactus mouse were equally abundant (Fig. 16). Neither *P. merriami* nor *C. eremicus* was captured here.

SEX RATIOS

The data on rodents collected from the 2.2-ha population plots are reported in Tables 7-10. Sex ratios on the population plots approached 1:1 for adults of all three species of pocket mice during every trapping interval except March when males predominated. Among Merriam's pocket mice the March prevalence of males over females was highly significant (0.01 probability level) when tested for chi-square (Table 22 in Porter 1962). The lopsided sex ratios in March were not significant for the other two species but the chi-square values in some instances were nearly significant. During December 1958 all three *P. merriami* and both *C. eremicus* trapped on the Merriami plot were males. Data for the habitat plots give a similar picture. On those plots, the preponderance of adult male over adult female *P. merriami* became highly significant during February. A preponderance of males over females was recorded for juvenile Merriam's pocket mice taken on the habitat plots during May. This discrepancy in numbers of male and female juveniles was also highly significant (Porter 1962). There was no divergence from a 1:1 ratio for either adults or juveniles of the other two species during any of the months in which samples were taken. Dixon (1959) also reported an early spring excess of males of *C. nelsoni* at Black Gap. Unbalanced sex ratios have been considered by

Table 7. Summary of the live-trapping of three 2.2-ha population plots (March 1958-July 1959). Total individuals captured includes animals for which the sex was not determined.

	Number of Individuals Captured			Percentage of Individuals Captured	Number of Times Captured		Percentage of Total Captures
	Male	Female	Total		Total	Mean	
MERRIAMI PLOT							
Perognathus merriami	69	46	115	46.7	469	4.0	46.8
Chaetodipus eremicus	9	5	14	5.6	41	2.9	4.1
Chaetodipus nelsoni	0	2	2	0.8	2	1.0	0.2
Dipodomys merriami	25	21	48	19.5	239	5.0	23.8
Peromyscus eremicus	33	25	60	24.4	244	4.1	24.4
EREMICUS PLOT							
Perognathus merriami	3	4	7	5.1	18	2.4	2.5
Chaetodipus eremicus	52	37	89	64.5	428	4.8	58.4
Chaetodipus nelsoni	0	0	0	0	0	0	0
Dipodomys merriami	15	15	31	22.5	259	8.3	35.3
Peromyscus eremicus	4	4	8	5.8	24	2.9	3.3
NELSONI PLOT							
Perognathus merriami	2	5	7	6.2	18	2.6	2.7
Chaetodipus eremicus	0	1	1	0.9	1	1.0	0.2
Chaetodipus nelsoni	37	30	67	59.8	446	6.7	67.9
Dipodomys merriami	0	1	1	0.9	2	2.0	0.3
Peromyscus eremicus	19	15	34	30.4	190	5.6	28.8

Table 8. Nelson's pocket mice individually marked and recaptured on the Nelsoni plot. Parenthetical numbers indicate additional uncaptured animals that were trapped in preceding and subsequent periods and assumed to be present on the plot but inactive during the trapping period. Superscript indicates two of the six adult males initially captured in March 1958 that died in the trap. Subsequent trapping periods in which mice of a given cohort survived and were recaptured can be determined by reading horizontally. Numbers of mice captured during a given trapping period and the cohort in which they were originally trapped and marked can be determined by reading vertically. Trapping period totals represent animals from all cohorts captured at least once during a given trapping period, with parenthetical numbers showing additional animals not captured but assumed present and inactive during that period. Each trapping period consisted of 16 nights of trapping, except the July 1959 period, which consisted of eight nights of trapping.

Marking Cohort	Age and Sex Class	Trapping Period					
		March 1958	July 1958	September 1958	December 1958	May 1959	July 1959
March 1958	Adult ♂	6[2]	0	0	0	0	0
	Adult ♀	3	2 (1)	2 (1)	1 (1)	1	0
July 1958	Adult ♂		8	2 (1)	1 (1)	1	1
	Adult ♀		6	4	2	2	1
	Juvenile ♂		2	1 (1)	2	2	1
	Juvenile ♀		2	1	0	0	0
September 1958	Adult ♂			1	1	1	1
	Juvenile ♂			2	0	0	0
	Juvenile ♀			3	3	1	1
December 1958	Adult ♂				5	4	4
	Adult ♀				4	2	1
	Juvenile ♂				1	0	0
May 1959	Adult ♂					3	1
	Adult ♀					1	0
	Juvenile ♂					4	2
	Juvenile ♀					8	5
July 1959	Adult ♂						1
	Adult ♀						2
	Juvenile ♂						4
	Juvenile ♀						1
Total trapped (all cohorts)		9[2]	20 (1)	16 (3)	20 (2)	30	26
	% inactive	0%	5%	16%	9%	0%	0%

Table 9. Merriam's pocket mice individually marked and recaptured on the Merriami plot. Parenthetical numbers indicate additional uncaptured animals that were trapped in preceding and subsequent periods and assumed to be present on the plot but inactive during the trapping period. Superscript indicates two of the 17 adult males initially captured in March 1958 that died in the trap. Subsequent trapping periods in which mice of a given cohort survived and were recaptured can be determined by reading horizontally. Numbers of mice captured during a given trapping period and the cohort in which they were originally trapped and marked can be determined by reading vertically. Trapping period totals represent animals from all cohorts captured at least once during a given trapping period, with parenthetical numbers showing additional animals not captured but assumed present and inactive during that period. Each trapping period in 1958 consisted of 16 nights of trapping, whereas the two 1959 trapping periods each consisted of eight nights of trapping.

Marking Cohort	Age and Sex Class	Trapping Period					
		March 1958	July 1958	September 1958	December 1958	May 1959	July 1959
March 1958	Adult ♂	17[2]	2	1	0	0	0
	Adult ♀	2	0	0	0	0	0
July 1958	Adult ♂		5	2 (1)	0 (2)	1 (1)	2
	Adult ♀		4	2	0 (1)	1	0
	Juvenile ♂		22	6 (2)	0 (5)	5	3
	Juvenile ♀		16	2 (5)	0 (5)	4 (1)	3
September 1958	Adult ♂			4	1 (1)	2	2
	Adult ♀			1	0 (1)	0 (1)	1
	Juvenile ♂			8	1 (3)	3	1
	Juvenile ♀			4	0 (1)	1	1
December 1958	Adult ♂				1	0	0
May 1959	Adult ♂					1	1
	Adult ♀					1	0
	Juvenile ♂					3	1
	Juvenile ♀					2	0
July 1959	Adult ♂						2
	Adult ♀						5
	Juvenile ♂						5
	Juvenile ♀						11
Total trapped (all cohorts)		19[2]	49	30 (8)	3 (19)	24 (3)	38
	% inactive	0%	0%	21%	86%	11%	0%

Table 10. Chihuahuan pocket mice individually marked and recaptured on the Eremicus plot. Parenthetical numbers indicate additional uncaptured animals that were trapped in preceding and subsequent periods and assumed to be present on the plot but inactive during the trapping period. Superscripts indicate three of the 10 adult males originally captured in March 1958 that died in the trap, either on their initial capture, or in the subsequent trapping period. Trapping periods in which mice of a given cohort survived and were subsequently recaptured can be determined by reading horizontally. Numbers of mice captured during a given trapping period and the cohort in which they were originally trapped and marked can be determined by reading vertically. No new or previously-marked Chihuahuan pocket mice were captured on the plot in December. Therefore, there is no December 1958 cohort, though 10 animals were presumed present but inactive. Trapping period totals represent animals from all cohorts captured at least once during a given trapping period, with parenthetical numbers showing additional animals not captured but assumed present and inactive during that period. The age was undetermined for two animals captured only during the September trapping period. Each trapping period in 1958 consisted of 16 nights of trapping, whereas the two 1959 trapping periods each consisted of eight nights of trapping.

Marking Cohort	Age and Sex Class	Trapping Period					
		March 1958	July 1958	September 1958	December 1958	May 1959	July 1959
March 1958	Adult ♂	10[2]	3[1]	1	0	0	0
	Adult ♀	3	2	0	0	0	0
July 1958	Adult ♂		3	0	0	0	0
	Adult ♀		1	1	0 (1)	1	0
	Juvenile ♂		20	9 (1)	0 (4)	4	1
	Juvenile ♀		13	4	0 (3)	3	1
September 1958	Adult ♂			2	0	0	0
	Adult ♀			4	0 (1)	1	0
	Juvenile ♂			7	0	0	0
	Juvenile ♀			5	0 (1)	1	1
	♂ not aged			1	0	0	0
	♀ not aged			1	0	0	0
May 1959	Adult ♂					6	1
	Adult ♀					3	0
	Juvenile ♂					1	0
	Juvenile ♀					2	0
July 1959	Adult ♂						1
	Adult ♀						2
	Juvenile ♀						3
Total trapped (all cohorts)		13[2]	42[1]	35 (1)	0 (10)	22	10
	% inactive	0%	0%	3%	100%	0%	0%

Elton et al. (1931) to be associated with breeding activities and with a greater tendency for males to wander more than females and hence to be more susceptible to capture than females during the breeding season. See Porter (1962) for further discussion of sex ratios on the population and habitat plots.

SEASONAL ACTIVITY PATTERNS

Dixon (1959) and MacMillen (1964) noted that cactus mice (*Peromyscus eremicus*) are much more susceptible to trapping during winter and early spring than during late spring, summer and fall, though Reichman and Van De Graaff (1973) found that trap success for this species in the Sonoran Desert of Arizona was slightly reduced in the winter. The present investigation revealed (Fig. 21) that cactus mice were much more commonly collected in the winter and early spring. Kangaroo rats were caught more frequently in the summer of 1959 than of 1958 (Fig. 21). In the case of cactus mice, some environmental factor affected by climate, such as fruit and seed production or insect populations, may be the causative factor. In field and laboratory studies, MacMillen (1965) found that cactus mice aestivate during summer when food or water is scarce, and are active at high temperatures (up to 38°C) as long as food and water are abundant. This aestivation has been shown to prevent water loss and extend food resources (MacMillen 1965). Reichman and Van De Graaff (1973) also found that activity of cactus mice was not adversely affected by high temperatures. The greater rainfall in July 1959 than July 1958 (Fig. 5) likely accounts for the greater activity of cactus mice in July 1959 (Fig. 21).

On the other hand, the increased activity of kangaroo rats in summer 1959 (Fig. 21) could be due to the lower temperatures in July 1959, compared with July 1958 (Fig. 5). Reichman and Van De Graaff (1973) and Reichman (1983) also observed that high temperatures affected the activity of kangaroo rats more than pocket mice, probably as a result of their larger body size.

Merriam's and Chihuahuan pocket mice were captured in greater abundance and comprised a greater percentage of individuals captured during late spring, summer and fall than did cactus mice (Fig. 21). The fact that pocket mice were attracted to bait in traps, whereas cactus mice were not, during the summer months when both pocket mice and cactus mice presumably were active, suggests that during these months there may be less competition between species for food than during spring and late fall when pocket mice and cactus mice were all susceptible to trapping.

Nelson's pocket mice were more active during the winter than the other two perognathine species (Fig. 21). During 784 trap nights (16 nights) in December 1958, 22 Nelson's pocket mice were assumed to occur on the Nelsoni plot. Twenty (91%) of this number were trapped in December (Table 8). During the December trapping period no *C. eremicus* were captured on the Eremicus plot and only three *P. merriami* (86% assumed to be inactive) were taken on the Merriami plot (Tables 9-10). The three Merriam's pocket mice, trapped in December, were captured only four times (two individuals were captured once each and one was captured twice). These four captures probably represented animals which became aroused from torpor to obtain food. Pocket mice likely do not remain in a torpid condition much longer than a week without food (Bartholomew and Cade (1957). In the laboratory, Bartholomew and Cade (1957) found that *P. longimembris* aroused at intervals of only a few hours to a day or more. MacMillen (1983) cites data from Meehan (1976) indicating that *Perognathus parvus* remain torpid during the winter, with torpidity of up to eight days interrupted by arousal for less than a day. It is likely then that most Merriam's and Chihuahuan pocket mice occasionally become active to obtain food. Consequently it is possible that only a few individuals present on the plot were active during any one night. If the plots had been trapped continuously throughout the winter, most of the individuals may have been captured at one time or another.

Manning et al. (1996) compared my results (as reported by Schmidly 1977a) with their data from the early 1990s for *C. nelsoni* and *C. eremicus* in the Big Bend region. They confirmed that unlike *C. eremicus*, Nelson's pocket mouse remains active throughout the

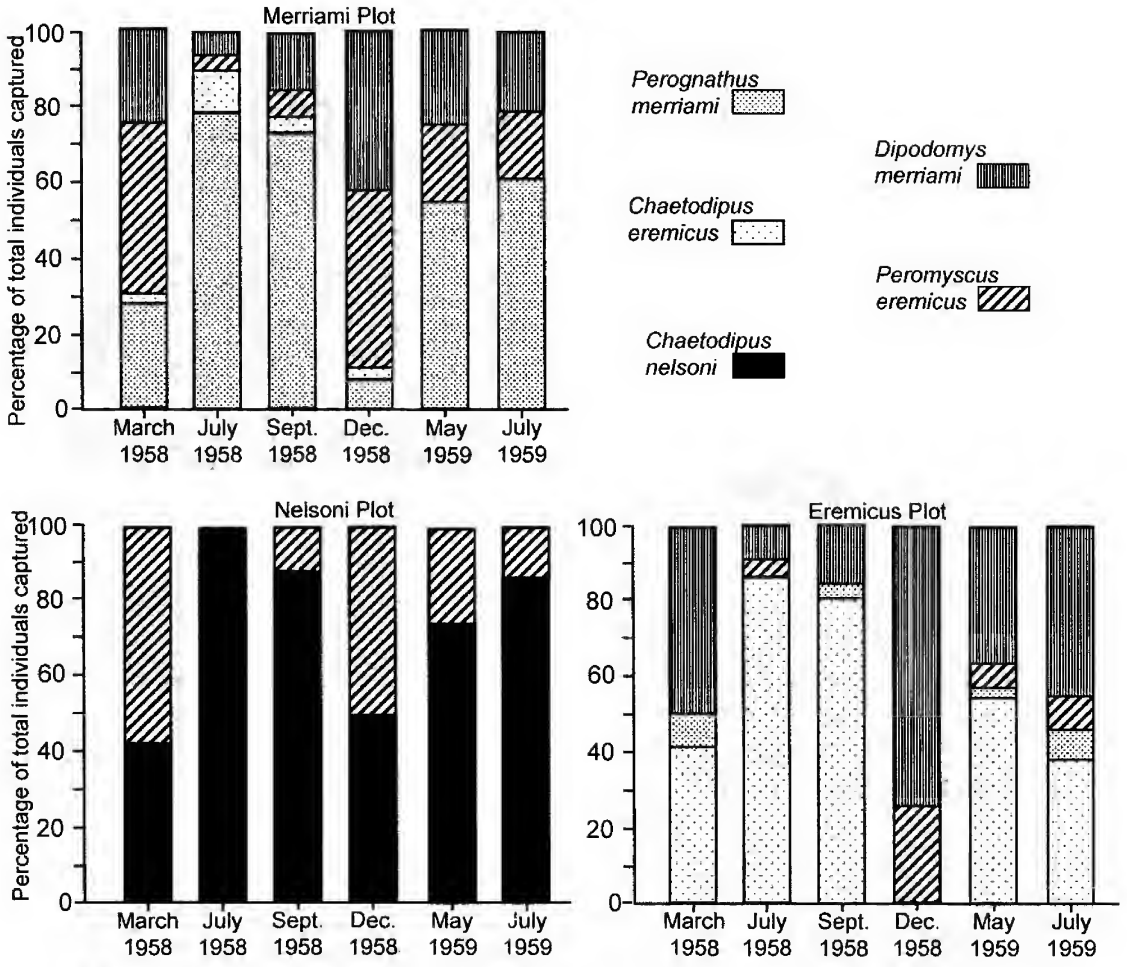

Figure 21. Relative seasonal occurrence of nocturnal rodents on the 2.2-ha population plots.

winter. Manning et al. (1996) also reported similar peaks of activity (July-September for Nelson's pocket mouse, and June-August for the Chihuahuan pocket mouse). They found that pocket mice were active in March during years of above average rainfall (1990-1992), but were inactive during March 1994, after a dry period.

Porter (1962) reported that captive *P. merriami* held at ambient temperature at Big Bend became torpid during the winter, with oral temperatures 1-2°C above ambient as long as environmental temperatures were above freezing. The mice apparently became active intermittently to feed. When temperatures dropped below freezing, *P. merriami* became continuously active. During trapping activities in December, February, and March, Merriam's pocket mice frequently were in a torpid condition in the traps. The Chihuahuan and Nelson's pocket mice seldom were observed in torpor. In February 1958, with temperatures ranging from 12.0°C to 26.2°C, six individuals of *P. merriami* and one of *C. eremicus* were trapped in a lethargic condition. Oral temperatures of the mice ranged from 1.0 to 3.2°C above ambient.

Field observations indicated that torpid Merriam's pocket mice were usually in traps in which the bait was exhausted. Bartholomew and Cade (1957) found that when their animals were removed from food for 24-36 hours, torpor was invariably induced regardless of the environmental temperature. According to Bartholomew and Cade (1957), aestivation in *C. eremicus* is

basically the same phenomenon as hibernation except that body temperature remains high because ambient temperatures are high. I found no pocket mice during this study that showed indications of aestivation.

Scheffer (1938) did not regard the dormancy displayed by *P. parvus* as true hibernation. According to Reynolds and Haskell (1949) hibernation does not appear to be equally developed in all species of pocket mice, with *P. baileyi* exhibiting weaker tendencies to hibernate than *C. penicillatus*. Bartholomew and Cade (1957) believe that torpidity, together with food storage and burrowing (as found in pocket mice), provides an effective adaptation for a small mammal living in an environment as severe and unpredictable as the deserts of North America. They point out that even with all food stores exhausted, individuals could survive a week or more at temperatures of 20-21°C. Accordingly, they believe that a small pocket mouse could survive even longer without food at 8°C because of the small amount of weight loss per day at low ambient temperatures. Bartholomew and Cade (1957) and MacMillen (1965, 1983) believe that torpidity is not as much an adaptation to temperature conditions as it is to adverse conditions when food is not readily available. It is assumed (Bartholomew and Cade 1957) that the ability of pocket mice to maintain normal behavior at low temperatures is of adaptive importance when they are active at temperatures near freezing. An additional adaptive advantage they did not mention is that it also places the mice under the ground and away from predation at a time prior to the critical spring period when, according to Leslie and Ranson (1940), Elton (1942) and Miller (1958) the adult population must be sufficiently large to provide a replacement large enough for the population to survive a high summer mortality and to establish a new vigorous overwintering population.

SEASONAL ABUNDANCE

Various methods can be used to estimate the size of rodent populations during a particular trapping period. The number of individuals actually captured during a trapping period is the simplest method, but does not include animals not captured because they are "trap-shy" or because they are inactive as a result of climatic conditions. Some rodents are never captured because it becomes increasingly difficult to capture the remaining residents as more and more animals are captured (Davis 1956).

A better estimate can be obtained by counting not only mice actually captured, but also those assumed to be present because they were captured during preceding and subsequent trapping periods (Miller 1958; Chapman and Packard 1974). However, for the first few trapping periods, there is no way to determine the number of inactive animals not trapped. This difficulty can be avoided by a modification (Dixon 1958) that includes only those animals that were recaptured in the same period or one of the following, and omits individuals captured only once.

Another method, a modification of the Lincoln Index (Davis 1956) involves marking and releasing animals for several days with a subsequent trapping of the plot to determine the proportion of previously marked to unmarked individuals. The following formula is used to estimate the population size: $N = Mn/m$; where

N = original unknown population,

M = number marked in first trapping.,

n = number caught in second trapping, and

m = number recaptured in second trapping.

A disadvantage in comparing populations with this method is that with confidence limits at the 0.05 level one can distinguish only large differences (Figs. 22-24) and estimates can vary greatly according to the duration of the trapping period. Davis (1956) recommends a five-day period of marking and releasing followed by a three-day period of trapping to determine the proportion of marked to unmarked individuals. He believes that after three days of the second trapping period new mice begin to infiltrate the area. An adequate period of trapping undoubtedly varies with the mortality and natality rates of the population. Trapping data from

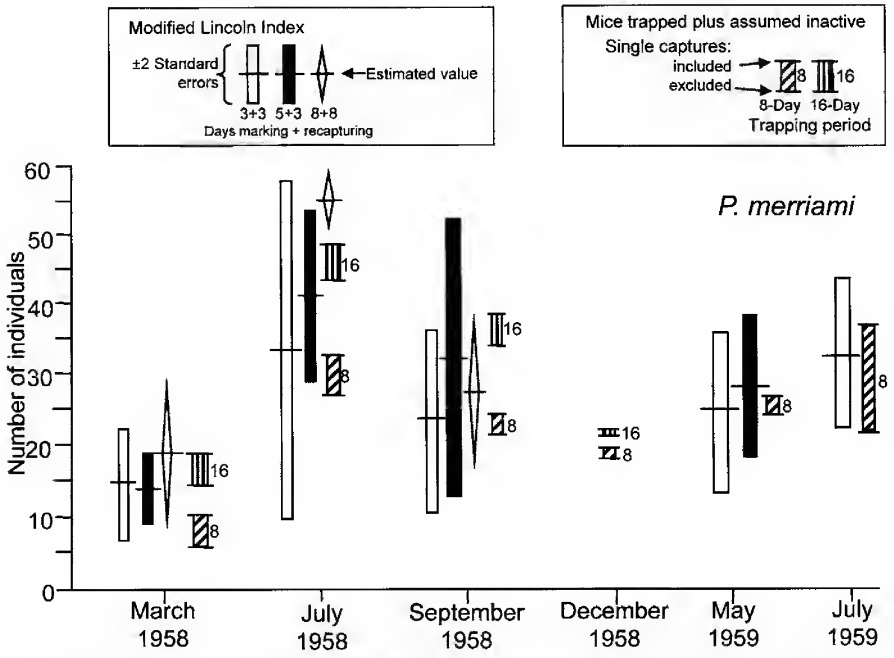

Figure 22. Seasonal population estimates for *P. merriami* on the Merriami plot based on modified Lincoln index and on the total mice trapped plus those assumed to be inactive because they were trapped during preceding and subsequent trapping periods. Modified Lincoln indexes are calculated based on 3+3, 5+3 or 8+8 (days of marking and releasing + days of recapturing) estimates. Horizontal center-lines indicate estimated values. Modified Lincoln Index estimates could not be calculated in December due to inactivity of the animals. The numbers of mice trapped plus assumed inactive are calculated both with and without omitting the single captures. The Merriami plot was trapped for only eight days during each of the 1959 trapping periods.

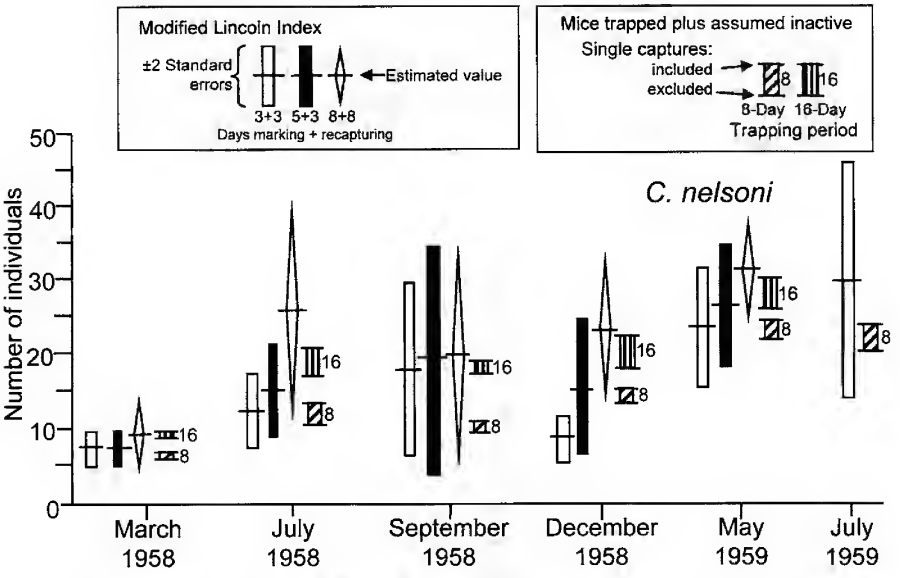

Figure 23. Seasonal population estimates for *C. nelsoni* on the Nelsoni plot. Calculations are explained in the text and in the legend for Figure 22. The Nelsoni plot was trapped for only eight days in July 1959.

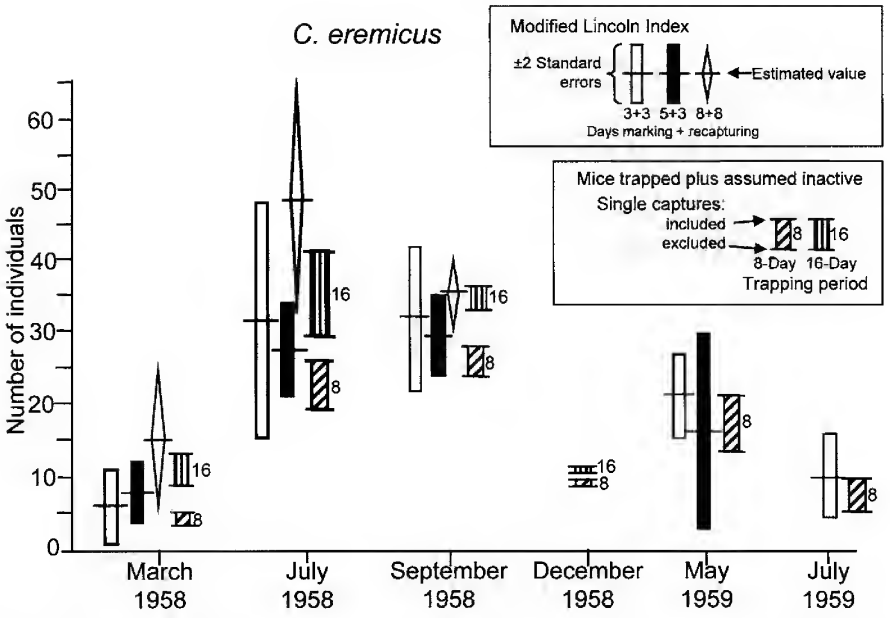

Figure 24. Seasonal population estimates for *C. eremicus* on the Eremicus plot. Calculations are explained in the text and in the legend for Figure 22. Modified Lincoln Index estimates could not be calculated in December due to inactivity of the animals. The Eremicus plot was trapped for only eight days during each of the 1959 trapping periods.

a population with a low turnover of individuals are less subject to error as a result of long trapping periods than from one with a high turnover. Distances between traps are also important in determining the duration of the trapping period. With traps spaced at greater distances it takes longer to sample a population than with traps set close together. Also "trap addicted mice" tend to cause the catch to be less random; consequently, one gets an underestimate of the population (Hayne 1949). This method is impractical for determining population density during periods of inactivity of the animal being studied.

Three population estimates based on the modified Lincoln Index of Davis (1956) were calculated for the population plots (Figs. 22-24). One was based on an eight-day mark and release period and an eight-day recapture period (8+8; open diamonds in Figs. 22-24). Another was calculated for a five-day mark and release period, followed by a three-day recapture period (5+3; closed rectangles in Figs. 22-24). The third estimate was based on a three-day mark and release period and a three-day recapture period (3+3; open rectangles in Figs. 22-24). These estimates were compared (Figs. 22-24) with 8-day and 16-day estimates based on assumed or known populations and on known populations less the single captures (Dixon 1958). The assumed or known populations were based on the number of individuals assumed to be present on the plot because they were captured during preceding and subsequent trapping periods.

In the 3+3 and 5+3 calculations, the first three trapping days of the first trapping period were considered as prebaiting days (Chitty and Kempson 1949). Since the traps were left on the plots between trapping periods and captures were relatively high on the first day of each subsequent trapping period, prebaiting was not deemed necessary for periods other than the first.

Long-term investigations of plots in marginal habitats where two or more species of pocket mice occur are needed to determine the correlation among such factors as (1) long and short term phenological changes of the habitat, (2) changes in long and short term population levels of age and sex classes for each species of pocket mouse residing on the area, (3) changes in the period and intensity of reproduction,

(4) food preferences of each species, and (5) nest and burrow requirements for each species. A study of this nature would answer many of the questions regarding the effects of these variants on the population levels of the species of pocket mice occupying the plots.

Abundance of Merriam's Pocket Mouse.—Population estimates were lowest in March 1958 and highest in July 1958 (Fig. 22). The small number of pocket mice recorded in March probably was due both to mortality and to lessened activity because of cold weather (Figs. 3-5; 21). The number of inactive mice could not be ascertained because March was the first trapping period. During the 16 trapping days in March and early April only 2 females and 17 males were captured (Table 9). This apparent lack of activity of females reduced the catch by almost half.

Only three animals were captured in December (16 trapping days), but at least 19 others were assumed to occur there because they were captured in preceding and subsequent trapping periods. In September, 30 animals were captured but 38 were assumed to occur on the plot (Table 9). Based on calculations for an 8+8-day trapping period these represent significant changes from the July total of 49 individuals (Fig. 22). The decrease in numbers in September may be attributable to lessened activity of the mice because of unusually high rainfall (9.8 cm) during the trapping period (Fig. 5A).

Abundance of Nelson's Pocket Mouse.—In March the number of *C. nelsoni* captured on the Nelsoni plot was low (9 animals for 16 days of trapping; Table 8). Although 21 individuals were known to occur on the plot in July, the known population was low compared with that of *P. merriami* (49) and *C. eremicus* (42) on their respective plots for the same period (Tables 8-10). Only a slight decrease in the known population of Nelson's pocket mice occurred in September.

In contrast to the other two species, Nelson's pocket mouse was active during December at which time more individuals were captured than in July 1958 (Fig. 23 and Table 8). Ten new animals (all but one were adults) appeared on the plot in December from an unknown source. The addition of 12 juveniles to the population in May 1959 (16 days of trapping) accounted for most of the increase in numbers during that period (Table 8 and Fig. 23). The number of animals trapped during the eight-day trapping period in July 1959 was the same as that in May (Fig. 23).

Abundance of the Chihuahuan Pocket Mouse.—On the Eremicus plot Chihuahuan pocket mice reached a peak of activity (numbers captured) in July 1958 (Fig. 24). The number of individuals captured on the plot decreased in September, and in December no pocket mice were trapped on the plot, although two individuals of *C. eremicus* were captured on the Merriami plot. At least 10 inactive individuals were assumed to be present on the Eremicus plot during December.

In May the active populations (numbers captured) appeared to be nearly back to the level reached in July 1958 (based on eight trapping days; Table 11), but in July 1959 the population was significantly smaller (Fig. 24). The cause of this decline is not known but it may have been the result of a marked decrease in the number of juveniles added to the population as compared with 1958 (Table 11).

Table 11. Numbers of pocket mice captured on the population plots during the first eight days of trapping. PTA = previously trapped adults; NTA = newly trapped adults; NTJ = newly trapped juveniles.

	Merriami Plot			Nelsoni Plot			Eremicus Plot		
	PTA	NTA	NTJ	PTA	NTA	NTJ	PTA	NTA	NTJ
March 1958	0	10	0	0	7	0	0	4	0
July 1958	2	5	28	1	12	0	3	6	17
September 1958	9	7	5	7	1	1	10	9	11
December 1958	1	1	0	5	9	1	0	0	0
May 1959	15	2	5	10	6	8	10	9	3
July 1959	14	7	16	16	3	5	4	3	3

BREEDING HABITS

Arnold (1942), Reynolds and Haskell (1949), and Scheffer (1923, 1938) discussed breeding in pocket mice. Scheffer (1938) believed gestation to be somewhere in the range of 21-28 days for *P. parvus*. Eisenberg (1963) and Eisenberg and Isaac (1963) reported gestation of 23-26 days for five species of pocket mice.

Determination of stage of reproduction in pocket mice as indicated by such external criteria as swollen vulva, perforate vagina, presence or absence of vaginal plugs, lactation, visible pregnancy, and scrotal testes were found to be inadequate, difficulties also noted by Chapman and Packard (1974). An attempt was made first to determine reproductive condition during the trap and recapture program of the population plots, but with little success. Later, animals taken from the habitat plots were examined for external indications of pregnancy and other reproductive criteria, but little if any correlation was found between these external criteria and the true reproductive condition of the animals. Handling of animals frequently caused testes to descend into the scrotal sacs. Hence, the following discussions are based on dissection and internal examination of animals taken from the habitat plots and the occurrence of juveniles on both the habitat and the 2.2-ha population plots. The presence or absence of embryos, the presence of fully formed spermatozoa in the testes and the average monthly weights of the testes were the criteria by which reproductive condition of the mice was determined. The presence of spermatozoa usually is considered indicative of fecundity even though the physiological condition of the spermatozoa cannot be established (Jameson 1950). It has been established that the testes increase in size as the mating season progresses, and they regress in size at its close (Jameson 1950). Unless otherwise noted, the data that follow were based on the examination of animals taken from the habitat plots during 1959.

Breeding Season of Merriam's Pocket Mouse

An increase in the reproductive activity of male Merriam's pocket mice from February to March 1959 was indicated by a rise in the average weight of the testes and a conspicuous increase in the percentage of animals having spermatozoa in the epididymides (Fig. 25A; Table 12). The testes acquired their greatest average weight in April, declined during the May-June period, and again increased in July. A sharp decrease in the breeding activity of males during August is suggested by the low weight of a testis from a single individual, and this is confirmed by small testis sizes in mice collected in August by Yancey et al. (2006) in the Harte Ranch area in the northern part of BBNP. An analysis of variance revealed no significant differences between the monthly means (Porter 1962). Data of Genoways et al. (1979) from the Guadalupe Mountains provide further evidence of a July peak in male reproductive condition followed by a gradual decline through October.

The first pregnancy was recorded in March and the first extensive captures of pregnant females were in April (Fig. 25A). The highest percentage of pregnant females was recorded in May. The incidence of pregnancy decreased sharply between May and June; during July and August no pregnant females were taken (Fig. 25A). Genoways et al. (1979) collected a female with two placental scars in the Guadalupe Mountains in June, and nonpregnant females in August and October. Yancey (1997) and Yancey et al. (2006) collected pregnant females from the Big Bend Ranch area in March, June, July, August, and October.

Although a few juvenile mice appeared in April, the first large influx of juveniles was in May (Fig. 25A) with a peak in June. In spite of the reduction in pregnant females after May 1959, the percentage of juveniles had not declined much by the first week of August. Consequently, one might infer that a second peak of sexual activity occurred during 1959. The increased weight of the testes in July supports this. There was a decrease in the percentage of young mice on the Merriami plot in September 1958 compared with July 1958 (Fig. 26). A very young individual was trapped on the Merriami plot September 24, and juveniles which had not yet entered the post juvenile molt were captured 7 October 1958. These young individuals probably were offspring of late breeding females rather than the result of a second peak of reproductive activity. The testes increased in weight noticeably about a month before

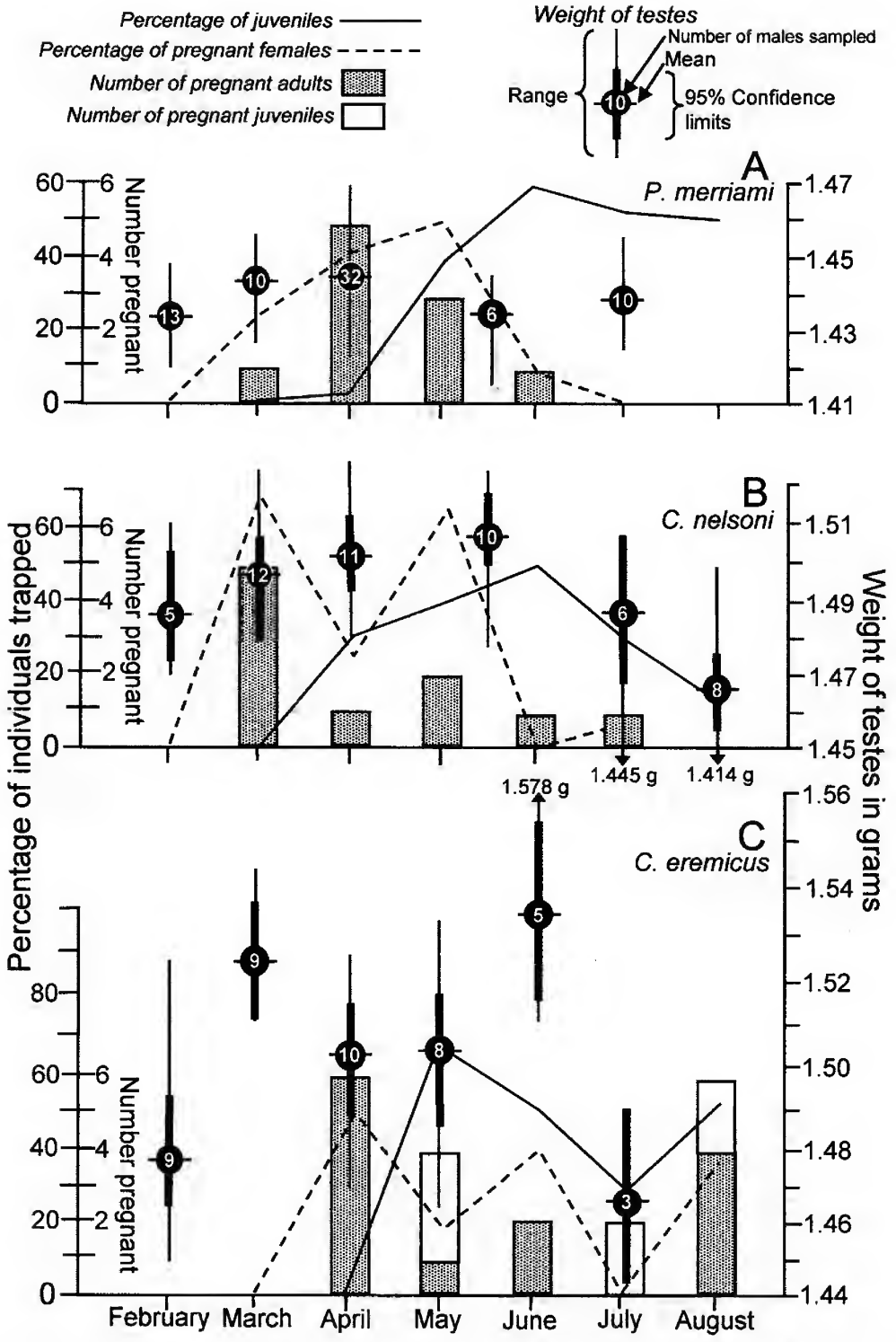

Figure 25. Correlation of the reproductive activities of three species of pocket mice on the habitat plots during 1959. A range that goes off scale is represented by an arrow with the high or low value shown. Confidence intervals were not calculated for *P. merriami*.

Table 12. Summary of the reproductive condition (in percent) of three species of pocket mice trapped on the habitat plots.

	Juvenile Females			Adults with Spermatozoa in Epididymis			
				1958		1959	
	Pregnant	Placental Scars	Juvenile Males with Spermatozoa (testes or epididymis)	February	March	February	March
P. merriami	0	0	30	11	100	31	100
C. nelsoni	10	5	0	80*	--	100	100
C. eremicus	20	2	7	--	67	67	100

*100% contained spermatozoa in their testes.

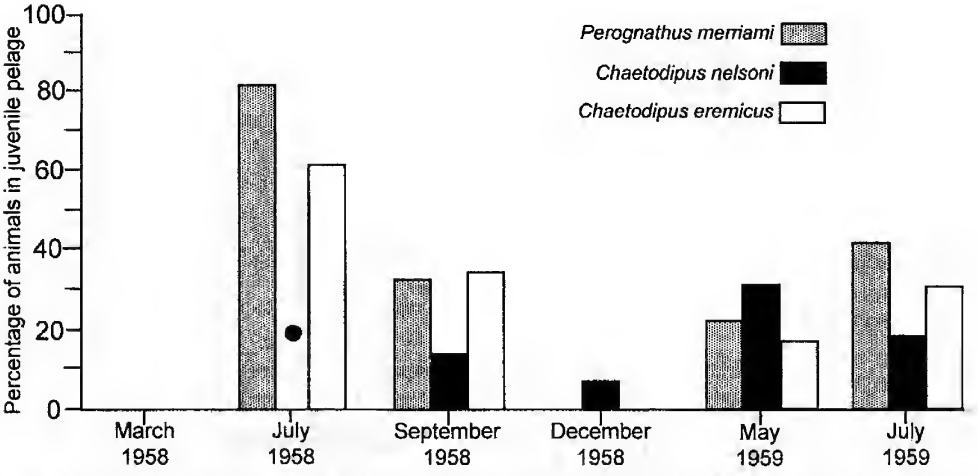

Figure 26. Seasonal percentage of animals in juvenile pelage in the pocket mouse populations on the 2.2-ha population plots, based on 8-day trapping periods. The black dot indicates percentage of juvenile *C. nelsoni* based on a 16-day trapping period in July 1958.

a marked number of gravid females was trapped. An influx of juveniles occurred about one month later. Peaks for each phase were also about one month apart (Fig. 25A).

Breeding Season of Nelson's Pocket Mouse

Spermatozoa were present in the epididymides or testes of all adult male Nelson's pocket mice trapped in February (Table 12). The testes showed a continual increase in average weight, beginning in February, and reached a maximum during the May-June period. In July the average weight declined to about the same value observed in February. During August the average weight of the testes sampled declined to a value significantly less than that observed during the previous months (Fig. 25B). Yancey et al. (2006) found similar results for this species in BBNP.

The percentage of pregnant females reached a peak in March, declined in April, reached a secondary peak in May, declined to zero in June and increased slightly in July (Fig. 25B). Yancey et al. (2006) collected pregnant females during June and August in the

Harte Ranch area of BBNP. Baker (1956) reported pregnancies from late March through July in Coahuila.

Juvenile Nelson's pocket mice first appeared in April, one month after the first pregnancy was observed. The largest percentage of juveniles was taken in June, after which their numbers declined conspicuously. An increase in the percentage of juveniles on the Nelsoni plot from 19% in July to 31% in September (Table 8) suggests a late July or August peak of pregnancy during 1958. This is also suggested by the fact that 78% of the individuals of this species trapped on the habitat plots late in August 1958 were juveniles. Very young animals were trapped on the Nelsoni plot on 26 September 1958, and juveniles which had not yet molted were recorded on October 7. During the December trapping period, one juvenile male was marked and released on the Nelsoni plot. An adult female taken 18 November 1957 on a habitat plot had enlarged mammary glands and showed signs of having nursed young. Thus it is probable that a few individuals are born as late as October or November, at least during warmer years. There was little correlation between the May-June peak of male breeding activity and the pregnancy peaks (Fig. 25B). However, the pregnancy peaks preceded by nearly a month the peak of occurrence of young. Yancey et al. (2006) found juveniles in BBNP in July and August.

Breeding Season of the Chihuahuan Pocket Mouse

Of the nine adult male Chihuahuan pocket mice taken in February 1959, 67% had spermatozoa in the epididymides (Table 12). By March all individuals examined had spermatozoa. Unlike the other two species, males of *C. eremicus* experienced two annual peaks in the size of testes. The average weight of the testes increased significantly between February and March (Fig. 25C), indicating a spring peak in the breeding activity of males, and decreased in April and May. In June the testes reached their greatest average weight, indicating a second peak in sexual activity. Subsequently the testes decreased in size and by July their average weight was significantly less than that for the peak months of March and June. Manning et al. (1996) and Yancey et al. (2006) also reported two peaks in testes size in this species from Big Bend, with the first peak occurring in March, but, the second peak not until August. The later date for the second peak could be due to different climatic conditions at the time of the study. In three of the four years of Manning et al.'s (1996) study, the Big Bend region experienced above average rainfall. My study of reproductive data was also conducted during a time of high rainfall (Fig. 6), particularly in late spring and early summer (Fig. 5). The long-term average annual precipitation in the Big Bend area for the period 1954-1960 (Fig. 6; Porter 1962) was 28.9 cm, as compared with 27.5 for the period 1961-1990 (Yancey 1997), suggesting that the baseline for what constitutes a year of average rainfall did not change more than 1.5 cm during the >30 years that intervened between the two studies. In New Mexico, Whitford (1976) found females in reproductive condition from February to September, with a peak in May, followed by occurrence of juveniles in June.

For Chihuahuan pocket mice, the first pregnancy and highest percentage of pregnancies were recorded in April (Fig. 25C). A second peak of pregnancy occurred in June and a third in August. The low incidence of pregnancy in May probably was attributable to the fact that the mice were collected near the Rio Grande where the reproductive periods probably occur earlier. Consequently a higher percentage of the catch was juveniles, and probably most of the adult females had already produced at least one litter. There was no indication of a decline in number of pregnancies in August. Yancey et al. (2006) reported pregnancies as late as September and November. In Mexico, Baker (1956) reported a pregnancy as early as February.

The first juveniles appeared in the traps during the latter part of May (Fig. 25C). A second peak of abundance was recorded in August. A definite decline in the percentage of young was recorded for the Eremicus plot between July and September 1958 (Table 10). Two very young individuals and several young animals in juvenile pelage were trapped on that plot in late September. Nearly a month elapsed between the first marked increase in the average weight of the testes (and also the first peak of pregnancy) and the first appearance of juveniles (Fig. 25C). Although some reproductive activity occurs throughout the months when this species is active, the data suggest two peaks of reproduction, one in spring and the second in late summer.

Discussion of the Extent of Breeding Season in Pocket Mice

The main reproductive period was in spring and, to a lesser extent, summer. There was a slight suggestion of both spring and late summer peaks of reproduction in all three species. These peaks were more pronounced in *C. eremicus* than in the other two species, especially at lower elevations where the weather warmed up earlier in the spring and stayed warm longer in the fall. Similarly, Reynolds and Haskell (1949) reported that in southeastern Arizona the breeding activity of *C. penicillatus* was highest in late spring, decreased during the drought period of June and early July, but increased again in August. They found that periods of greatest sexual activity were concurrent with seasons of new vegetative growth of spring and summer. A similarly divided breeding season, observed by Reynolds (1960), in *Dipodomys merriami* in the same general area of Arizona likewise corresponded closely with the periods of new vegetative growth of spring and late summer. As pointed out by Reynolds (1960), who cited Bodenheimer and Sulman (1946), there is some evidence that nutrients contained in fresh vegetation have a stimulating effect on the breeding activity of rodents. Holdenried and Morland (1956) found that 77 pregnancies in *Perognathus flavus* were distributed as follows: January—0; February—2; March—0; April—11; May—10; June—29; July—8; August—1; September—10; October—6; November and December—0. Hence there were also two reproductive periods in *P. flavus*. The double peak may be a widespread phenomenon among heteromyid rodents for the southwestern deserts where spring and fall periods of precipitation are the rule. A more detailed study of the reproductive activity of *Perognathus* and *Chaetodipus* in the Big Bend area is needed to verify the presence or absence of a divided period of sexual activity. In all three species, reproduction appeared to begin abruptly in the spring and to taper off gradually in the fall.

Breeding activities of *C. nelsoni* began about one month earlier in the spring of both 1958 and 1959 than did those of the other two species. Likewise, Nelson's pocket mice bred later in the fall than did the other species. The longer breeding period of *C. nelsoni* is probably correlated with the species' winter activity pattern. Manning et al. (1996) and Yancey et al. (2006) collected pregnant females of *C. nelsoni* during June and August in the Big Bend region, and they found juveniles throughout the summer and as late as November. For *C. eremicus*, they reported pregnant females nearly every month from March though November.

The onset and duration of reproduction appear to be associated with phenological conditions of the habitat. Hence, these phenomena vary from year to year with those conditions rather than with calendar dates (Brown and Harney 1993). The reproductive season in 1959 began nearly one month earlier than it did in 1958. A greater percentage of adult male *P. merriami* and *C. eremicus* contained spermatozoa in the epididymides during February 1959 compared with February 1958 (Table 12). The difference between the two years is less evident in male *C. nelsoni* probably because its breeding begins earlier. The later breeding season in 1958 is further pointed up by the later emergence of female pocket mice compared with 1959. This fluctuation was also noted by Dixon (1958) who found that the March 1957 population values for the Black Gap area (see Fig. 2) were more similar to those for April 1958 than to those for March of that year. He also recorded a greater trap response for *C. nelsoni* in March 1957 than at comparable calendar dates a year later. Further, he recorded juveniles earlier in 1957 than in 1958. During January-March 1957 the average temperatures at Panther Junction were conspicuously above normal whereas a year later they were well below normal (Fig. 5)

Analysis of Numbers and Uterine Distribution of Embryos and Placental Scars

The difference in the average number of embryos or placental scars recorded for each of the three species of pocket mice (Table 13) was small. Nelson's pocket mouse had a slightly smaller average number of embryos per female than did the other two species, and *C. eremicus* had a somewhat higher average number of placental scars than either of the others. Baccus (1971) reported similar mean numbers of embryos in *P. merriami* (3.7 embryos, ranging in number from 3 to 5) and *C. eremicus* (3.5 embryos, ranging in number from 2 to 5) in BBNP, but found slightly larger litters (4 embryos in each of two pregnant females) in *C. nelsoni*. Yancey

Table 13. Number of embryos and placental scars of three species of pocket mice.

	Number of Embryos			Number of Placental Scars		
	Sample Size	Range	Mean	Sample Size	Range	Mean
P. merriami	10	1-4	3.6	19	2-21	5.9
C. nelsoni	12	2-4	3.2	19	2-10	5.1
C. eremicus	23	2-6	3.6	31	2-19	7.4

et al. (2006) reported a mean of 4 embryos (range 3-5) in *C. nelsoni* and 3.6 (range 2-6) in *P. merriami* in the Harte Ranch area of BBNP.

The average of 3.6 (range 2-6) embryos per female recorded for *C. eremicus* in this study is similar to the 3-4 embryos reported by Baker and Greer (1962), the 3.5 embryos (range 2-5) by Baccus (1971), and 3 embryos by Genoways et al. (1979), but slightly smaller than the 4.4 (range 2-8) reported by Yancey et al. (2006). The number of embryos and placental scars I observed in each uterine horn did not differ significantly from a ratio of 1:1 (see Porter 1962). *C. eremicus* had an average of 2.0 embryos in the right horn and 1.6 in the left.

Incidence of Breeding in Juveniles

There was considerable difference among the three species in their ability to reproduce before acquiring adult pelage. None of the juvenile female Merriam's pocket mice examined was pregnant or had placental scars. Conversely, 30% of the young males had spermatozoa either in the testes or in the epididymides (Table 12). Males of the other species were less sexually precocious. Only 7% of the juvenile males of *C. eremicus* had spermatozoa in their gonads. Females of *C. nelsoni* and *C. eremicus*, however, were more precocious than those of *P. merriami* (Table 12). There was a much higher evidence of reproductive activity in juvenile males of *P. merriami* than in juvenile males of the other species which was difficult to explain.

LONGEVITY

The data were not suitable to construct life tables because animals were inactive during the winter and the trapping periods were too infrequent. However, information was compiled on longevity for the three species of pocket mice. Mortality estimates based on trapping data would represent the upper limit of mortality, since the data cannot distinguish between individuals that died and those that dispersed from the plot (Brown and Harney 1993).

Merriam's Pocket Mouse

The annual turnover in the population of *P. merriami* on the Merriami plot from July 1958 to July 1959 was somewhat greater (84%) than that reported by Dixon (1958) at Black Gap (75%). The annual probability of living was 0.16 (16% of the population would probably live one year) on the Merriami plot. Of the seven adult males captured on the Merriami plot in July 1958, 29% (2 animals) survived until July 1959 (Table 9). A slightly lower percentage (16%) of the juveniles survived a full year (males 14% and females 19%) than of the adults (18%).

Considering the small size of Merriam's pocket mouse, its longevity is much higher than normally would be expected. Dixon (1958) recorded a maximum life span of 33 and 22 months, respectively, for two mice at Black Gap. He recorded 25% survival of 24 mice which were marked 12 months or more before the last trapping period. Of these, the ones living the longest were immature when marked; a male was recorded for 89 weeks and a female for 96. On the Merriami plot, one animal was first captured as an adult

(at least a year old) in March 1958 and last recorded in September 1958. Two males, first captured as adults in July 1958, were taken again during the last trapping period (July 1959) and were suspected of being at least 15 months old and possibly older. Of 38 young mice, first marked in July 1958, 6 were still alive in July 1959. They were also approximately 15 months of age when last recorded.

Nelson's Pocket Mouse

Dixon (1958) reported an annual turnover of nearly 75% in the population of *C. nelsoni* at Black Gap which is somewhat lower than I recorded for this species on the Nelsoni plot (86%). The annual probability of living was 0.14 for *C. nelsoni* on the Nelsoni plot. The percentage of adult males (13%) that survived a year was similar to that for adult females (11%) whose "life span" was at least one year. A greater percentage of juveniles (25%) than of adults (14%) survived from July 1958 to July 1959. At Black Gap, Dixon (1958) found *C. nelsoni* to be unusually long-lived. He recorded two individuals which survived 30 months, one 24 months and two others about 20 months.

Data from the Nelsoni plot were similar. An adult female, first taken in March 1958 and last trapped in May 1959, was at least 20 months old (Table 8). Of 14 adults taken in July 1958, two survived to July 1959, at which time they were at least 15 months old. One of four juveniles marked in July 1958 was taken a year later when it was at least 13 months old (Table 8).

Chihuahuan Pocket Mouse

The annual turnover in the population of this species (95%) was greater than that of the other two species. The probability of living at least one year was correspondingly low (0.05). An 81% turnover was recorded from July 1958 to May 1959. None of the animals marked as adults in July 1958 survived to July 1959, although one was recorded in May (Table 10). Only 7 of the 33 juveniles marked in July 1958 were recorded in May 1959, and only 2 were recaptured in July. One of the oldest known individuals which was an adult in March 1958, was recaptured in September. This animal was at least 12 months of age. A young male and a young female, first captured in July 1958, were known to have survived more than a year.

Discussion and Comparisons of Longevity

A remarkably high percentage of the individuals of *P. merriami* and *C. nelsoni* marked in July 1958 was recaptured in July 1959. That *P. merriami* showed the smallest turnover in population is particularly interesting because of its small size. Chihuahuan pocket mice were not as long lived as Merriam's and Nelson's pocket mice. The high survival rate of pocket mice in desert scrub areas might be attributed to food storage and hibernation (Dixon 1958) and better cover. Mild winters in the southern deserts also play an important role in survival of these rodents. The differences between the survival of pocket mice at Black Gap and in BBNP may be associated with more severe winters and longer trapping periods in the latter area.

Except for *C. eremicus*, the longevity of pocket mice was greater than usually encountered among small rodents (Blair 1953). In California, Fitch (1948) found that only 5% of the *Dipodomys heermanni* population survived one year or more. Burt (1940) reported that only 4% of 1,382 *Peromyscus leucopus* survived a full year in Michigan. Out of 559 individuals of the same species trapped by Snyder (1956) in Michigan only one individual survived a year. Snyder also showed that 15.8% of the mice marked while only a few weeks old lived 53 weeks under one set of environmental conditions, but only 1.8% survived 53 weeks under more severe conditions. In England, Evans (1942) reported that in marked populations only 1% of the *Myodes glareolus* and 1% of the *Apodemus sylvaticus* were trapped a year after the original capture. But in 1941, Manville (1949) recaptured 34% of the *P. maniculatus* he had marked in 1940, and 14% of the mice marked in 1941 were retaken a year later.

Figure 27 shows the percentage of July 1958 captures on the 2.2-ha population plots that survived to subsequent trapping periods. The low survival rate of *C. eremicus* was probably related to the substantial loss in numbers between July and September 1958. The rate of decline in the percentage of surviving *C. eremicus* parallels that for *P. merriami* for the December and May trapping periods. Although a larger percentage of

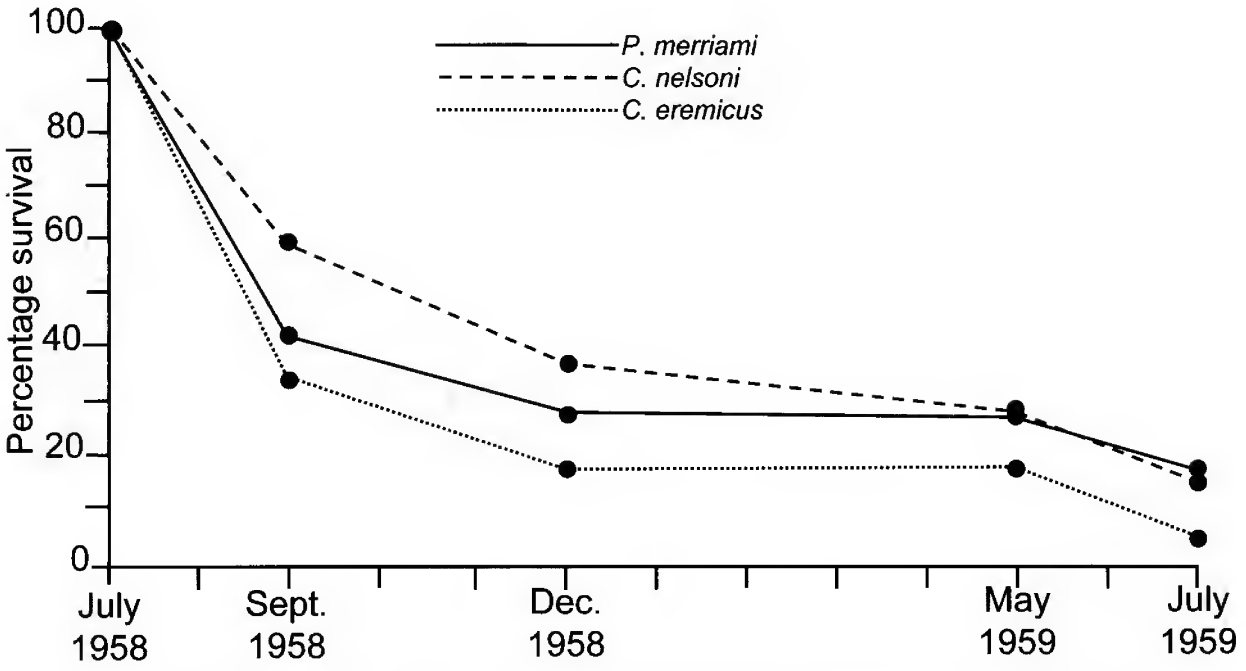

Figure 27. Seasonal survival of cohorts of three species of pocket mice from July 1958 to July 1959.

C. nelsoni survived between July and September 1958 as compared with *P. merriami*, the rate of decline or *C. nelsoni* between May and July 1959 was slightly greater than for *P. merriami*. Most of the mortality or loss to the populations of all three species took place between July and December 1958.

PELAGE CHANGES

Hansen (1954) discussed molt patterns among genera of ground squirrels and found three basic types. The "diffuse type" of *Urocitellus* occurred once a year and was characterized by the lack of a molt line. The second type, found in *Callospermophilus* and *Otospermophilus*, was also a single annual molt, but with a distinct molt line and with hair replacement on the head and shoulders before the molt line appeared. The third type, found in *Ammospermophilus*, *Ictidomys*, and *Xerospermophilus*, had two hair replacements annually yielding winter and summer pelages. The molt patterns in pocket mice resembled the second type described by Hansen but with certain noteworthy differences among the species.

Progression of Molt

Although different in details, the general pattern of molt in the three species of pocket mice was similar in that it progressed from the head posteriorly and terminated at the ankle (Fig. 28). The venter usually did not have an evident molt line and the rate of molt was slower there than on the dorsum. Consequently, by the time the dorsal molt line reached the rump the ventral molt was still in the region of the belly. As a result, the final stages of molt in all three species was characterized by a molt line extending from the rump laterally and anteriorly across the thighs and sides (Fig. 28D 4). The molt then progressed posteriorly on the

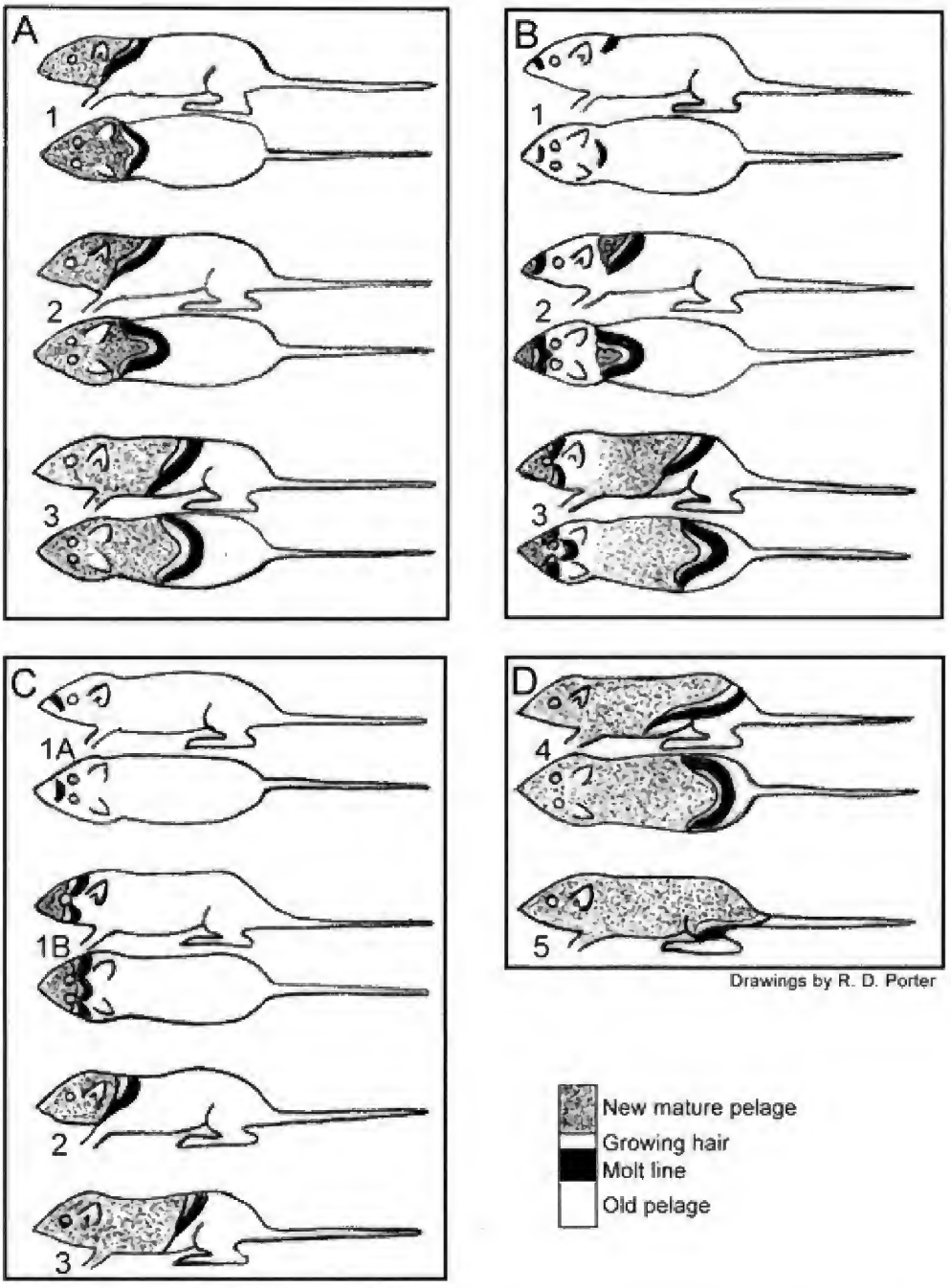

Figure 28. Sequence of molt of three species of pocket mice. Numbers indicate successive stages of molt. A. *Perognathus merriami*. B. *Chaetodipus eremicus*. C. *Chaetodipus nelsoni*. D. Final stages of molt for all three species.

belly and down the hind legs. The last stage of molt was indicated by molt lines near the ankles (Fig. 28D 5).

The dorsal molt lines originated in different areas on each of the three species (Fig. 28A-C). In Nelson's pocket mouse, it started on the nose and progressed posteriorly (Fig. 28C). In Merriam's pocket mouse, a molt line usually did not appear until the head region was covered completely with new mature hair (Fig. 28A 1). Only one individual of this species was observed to have a molt line on the head. Most *C. eremicus* observed during this investigation had two dorsal molt lines, one generally originating on the nose as in *C. nelsoni* and the other on the neck as in *P. merriami* (Fig. 28B 1). The molt line originating on the nose progressed posteriorly until it disappeared in the new hair of the neck. It usually reached the posterior part of the head about the same time the second molt line reached the rump (Fig. 28B 3). There were no observed differences in the sequence of molt between juveniles and adults of the same species. Speth (1969) reported that the Great Basin pocket mouse, *P. parvus*, begins its molt behind the ears, and with a second area of molt originating later on the nose.

Size of Juveniles at Time of Molt

Juveniles of all three species molted directly into adult pelage. There was considerable variation in the size of individual animals when the molt line first appeared. Juveniles of *P. merriami* and *C. nelsoni* in molt were intermediate in size between juveniles not in molt and adults, as measured by weight and body length (Fig. 29). In these two species, juveniles completed the postjuvenile molt before they have acquired their mature weight and body length. On the other hand, young Chihuahuan pocket mice observed in molt were nearly as large as adults (Fig. 29). This probably accounts for the higher percentage of pregnant juveniles recorded for *C. eremicus* than for the other two species. Juvenile *C. eremicus* not in molt were significantly smaller than molting juveniles and adults (Fig. 29).

Duration and Season of Molt

My observations of a single annual molt in adult pocket mice are in general agreement with those of Osgood (1900). Kangaroo rats also follow this pattern (Grinnell 1922). On the other hand, Great Basin pocket mice (*P. parvus*) from Utah molt semiannually (Speth 1969), with the first molt beginning in January or February and concluding in March or April. The summer molt in that species begins in June and is completed by August or September. I examined a dozen or more mice per month of each species beginning in February, and found no evidence of a late winter molt in any of the Big Bend pocket mice (Fig. 30).

For most juveniles and adults the duration of molt was one month or less. Some juveniles which were about half their mature weight and sparsely haired ventrally completed the molt within a period of 30-45 days. A juvenile female Merriam's pocket mouse, for example, which was sparsely haired beneath and showed no signs of molt when first captured on 25 July 1958, had completed her molt by 6 September. A young male *C. eremicus* which had no indications of molt on 5 July 1958 had completely molted by 29 July. It was first observed in molt on 13 July when it was in a stage similar to Fig. 28B 3. Most individuals captured in juvenile pelage in July 1958 had completed the postjuvenile molt when recaptured in September. Two or three juveniles of *P. merriami* and of *C. nelsoni* captured during the last week in May 1959 had not yet completed the postjuvenile molt when recaptured 9 July 1959. The duration of molt is similar to that seen in *P. parvus*, which generally takes 30-35 days to complete its molt, with a range between 11 and 90 days (Speth 1969).

For adult pocket mice the annual molt takes place from May through October in Big Bend (Fig. 30). More recent studies by Genoways et al. (1979), Manning et al. (1996), and Yancey et al. (2006) indicated similar periods of annual molting, with molting specimens of Nelson's pocket mouse collected June-August, Chihuahuan pocket mice molting in June through October, and Merriam's pocket mice collected in molt during June-August. In Washington, Scheffer (1938) found that by the end of August 65% of the males of *P. parvus* were in molt, but only an occasional female. He found that females reached their peak of molt 3-4 weeks later. There did not appear to be any difference between sexes as regards the peak of molt in the three species occurring in the Big Bend area.

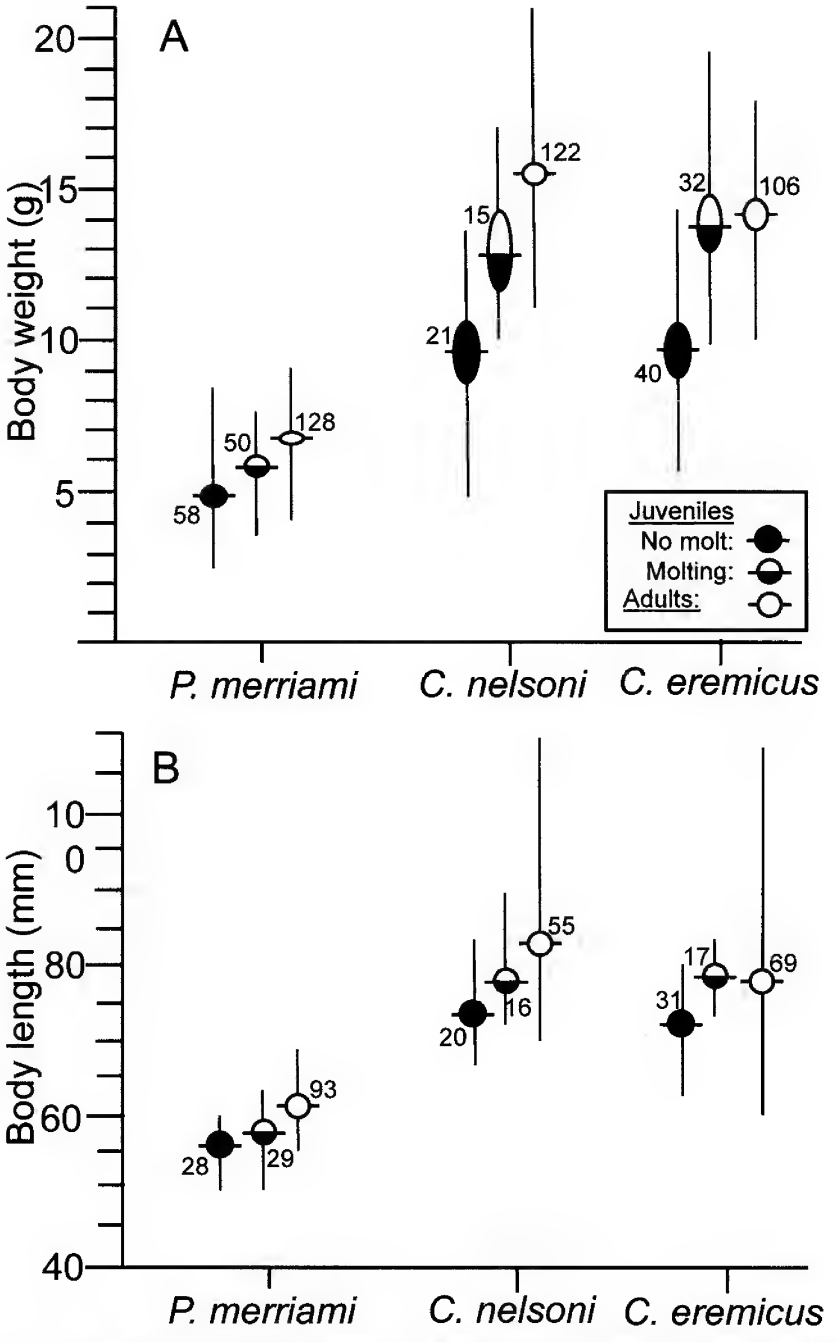

Figure 29. Size of juvenile pocket mice with and without molt compared with adults. Horizontal lines indicate mean values. Vertical lines indicate ranges. Numbers indicate sample size. For both weight and length, adults and molting juveniles of *C. eremicus* show no significant differences in weight. All other pelage classes show significant differences within species. A. Body weight. Height of symbol indicates 95% confidence intervals. B. Body length.

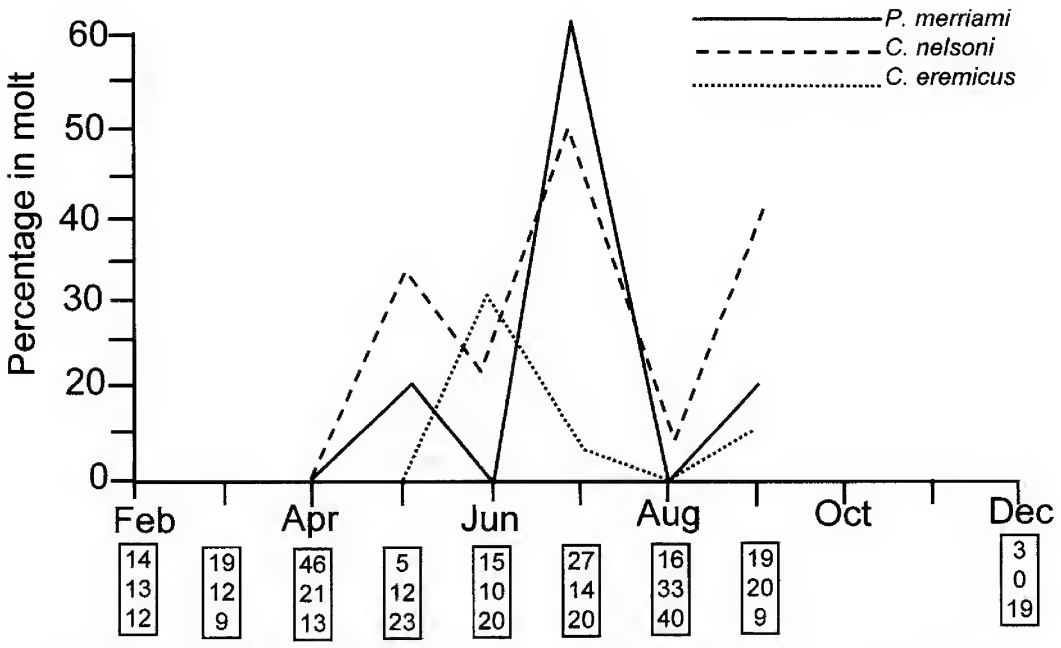

Figure 30. Seasonal incidence of molt in three species of pocket mice. Numbers in rectangles indicate the number of animals examined for molt, with *P. merriami* on the top, *C. eremicus* in the middle, and *C. nelsoni* on the bottom. None of the mice collected in February, March, April, or December were in molt. No specimens were examined in January, October, or November.

SPATIAL ORGANIZATION

Home Range

The home range of an animal is that area which it habitually traverses during its normal daily activities (Burt 1943; Blair 1953). This definition excludes occasional sallies outside the area for exploration or establishment of a new range. A variety of methods have been employed to determine home range in wild populations. The most accurate method is direct observation, but with nocturnal rodents this is impractical. Consequently, the size of home range usually is estimated by recording the places of capture of marked mice in live traps arranged in grid. The most distant traps in which the animal is taken determine the limits of the trap-revealed range. Hayne (1949) describes a home range as revealed by trapping as "an area over which the animal enters traps with greater or lesser frequency according to the location of the traps."

Doubt exists in the minds of some regarding the validity of this method, since Hayne (1950) and Stickel (1954) have found that there is a positive relationship between the ranges revealed by trapping and the distance used between traps. Despite this apparent fault, Blair (1953), among others, contends that peripheral points of capture are a fairly reliable estimate of the home range. Some methods allow the data of a large number of animals to be considered, whereas other procedures deal with only those individuals that enter the traps a large number of times (Brown 1956). Estimates of home range derived from calculating the area enclosed within peripheral points of capture require a large number of captures. Blair (1942) found that for *Peromyscus maniculatus* 10 or more captures were necessary to reveal the maximum home range. Godfrey (1954) found that 16-19 records from her Geiger counter were needed before she was able to obtain maximum values for *Microtus agrestis*. Conversely, the extent of movement may be ascertained by presentation of the data as distances between points of capture rather than as areas occupied. With this method, only the distances between two or more captures are needed.

Measurements from most of the captures may thus be used in analyzing the data.

In this report the mean recapture distances were compared on a seasonal (trapping period) basis for the age and sex classes of each species (Figs. 31-34). Trap-revealed home ranges were compared for adult males, adult females and juveniles of each species captured six or more times (Fig. 31). A mean range was calculated for each of these groups and for every trapping period using the exclusive boundary strip method (Stickel 1954). The calculated home ranges were then averaged together irrespective of the trapping period from which they came. In his studies, Hayne (1949) estimated a "center of activity" which is the geographic center of all points of capture. Blair (1951) believes that a better term for such a point is "average point of capture." The center of activity was estimated for each pocket mouse captured during each of two or more trapping periods. Distances were calculated between centers of activity from one period of capture to the next and from the period of first capture to each subsequent period for the purpose of measuring the amount of shift in relative position of individual home ranges during the course of the investigation. Data on home range and shifts in center of activity are presented in Figs. 31-35 and in Tables 39-53 of Porter (1962).

According to Blair (1953), young animals that have recently ventured from their nests apparently range over smaller areas than do adults. As the juveniles approach sexual maturity, some of them may disperse, apparently to set up residence elsewhere (Brown 1956). Howard (1949) found that some young *Peromyscus maniculatus* moved as much as 1 km when they became sexually mature, whereas other juveniles set up residence in the area of their birth. Reynolds (1960) reported that young *Dipodomys merriami* ranged over a significantly smaller area than did adults.

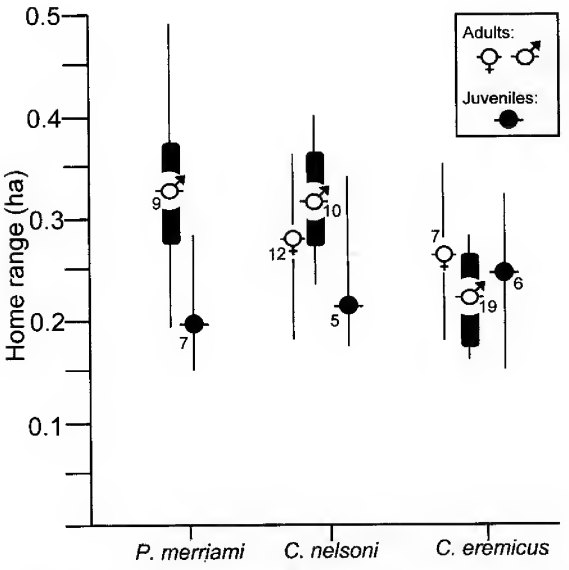

Figure 31. Home range of sex and age classes of individuals of three species of pocket mice captured six or more times. Horizontal bars indicate mean values. Vertical lines indicate the range. Vertical bars indicate 95% confidence limits comparing adult males. Sample sizes are indicated with numbers. Adult males of P. merriami differ significantly in their home range from both juvenile *P. merriami* and adult male *C. eremicus* (see Porter 1962).

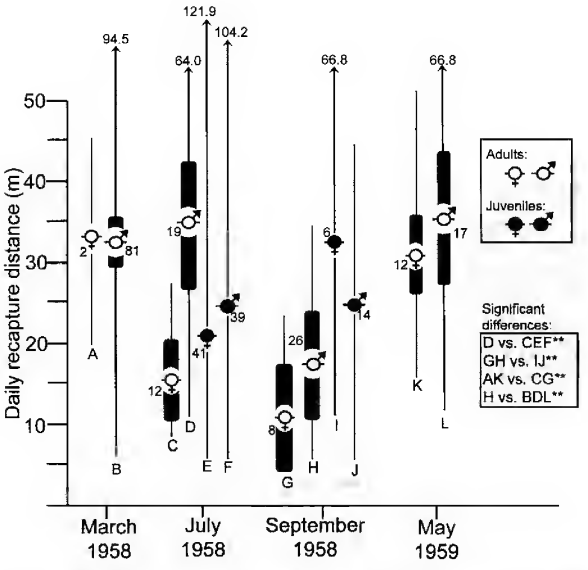

Figure 32. Daily recapture distances in Merriam's pocket mouse. Horizontal lines indicate mean values. Vertical lines indicate the range with maximum recapture distances indicated for values that go off scale. Vertical bars indicate 95% confidence limits comparing adult classes represented with large sample size (sample size indicated next to each symbol). Significant differences (all at the 0.01 level of probability) based on an analysis of variance (Porter 1962) are listed.

Brown (1956) suggests that once individuals of certain rodent species have established their home ranges they seldom move from these positions, except for occasional exploratory trips from which they return. Males of many species of rodents range more widely than do females presumably because of the female's greater attachment to the nest and young (Blair 1953). Blair (1943) found this to be the case with the Chihuahuan pocket mouse, as did Dixon (1959) with adult male *C. nelsoni*. Females of a few species range more widely than do males (Blair 1953). York (1949), for example, estimated a much larger average home range among adult female Merriam's pocket mice than he did among adult males. His sample size, however, was too small to indicate statistical significance.

Among other rodents, such as kangaroo rats (*Dipodomys*), there does not appear to be a sex difference in size of home range (Blair 1953). Blair (1943) investigated *Dipodomys merriami* and *D. ordii* in New Mexico; Fitch (1948) studied *D. heermanni* in California, and Reynolds (1960) reported on *Dipodomys merriami* in Arizona. None of these studies showed sex differences in the size of home range. Conversely, York (1949) found that male *Dipodomys merriami* ranged more widely than did females in western Texas. But his results were based on a small number of samples.

Home Range of Merriam's Pocket Mouse.— There were no significant differences in the mean recapture distances between the adult males and adult females for the month of May 1959. During July 1958, however, the mean recapture distance of adult males was significantly greater than it was for adult females and for juveniles of both sexes (Fig. 32). In September, juvenile females moved significantly greater distances on the average than did adults (Fig. 32). Juvenile males moved significantly greater distances than did adult females.

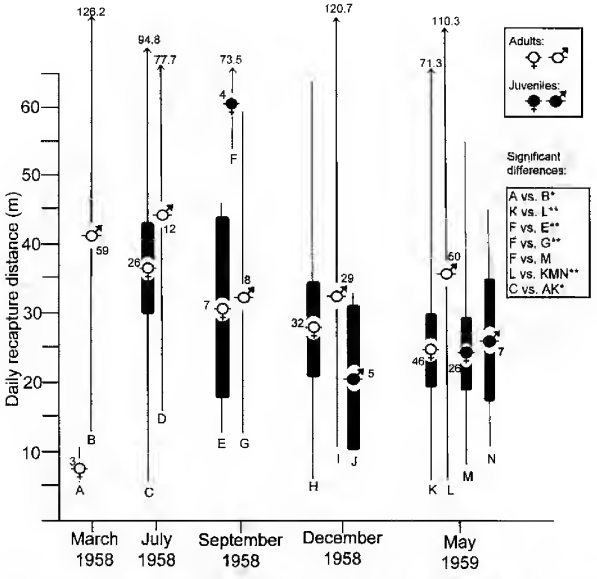

Figure 33. Daily recapture distances in Nelson's pocket mouse. Horizontal lines indicate mean values. Vertical lines indicate the range with maximum recapture distances indicated for values that go off scale. Vertical bars indicate 95% confidence limits for selected classes. Sample sizes are indicated next to each symbol. Significant differences at the 0.05 (*) or 0.01 (**) levels of probability based on an analysis of variance (Porter 1962) are listed.

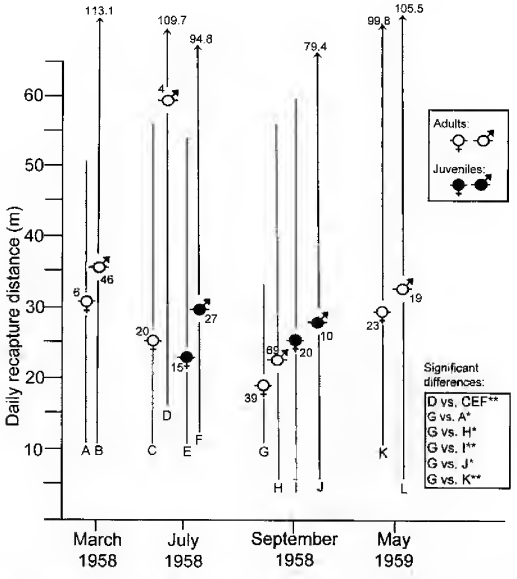

Figure 34. Daily recapture distances in the Chihuahuan pocket mouse. Horizontal lines indicate mean values. Vertical lines indicate the range with maximum recapture distances indicated for values that go off scale. Sample sizes are indicated next to each symbol. Significant differences at the 0.05 (*) or 0.01 (**) levels of probability based on an analysis of variance (Porter 1962) are listed.

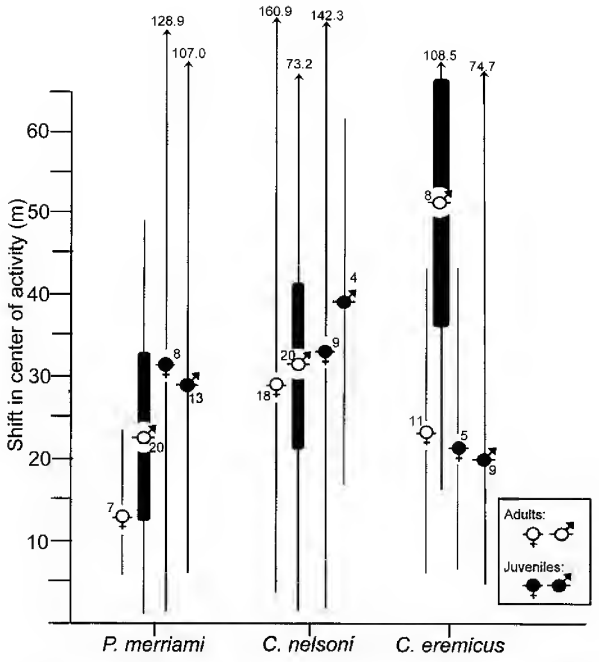

Figure 35. Shift in center of activity from one period of capture to the next in three species of pocket mice. Horizontal lines indicate mean values. Vertical lines indicate the range with maximum recapture distances indicated for values that go off scale. Vertical bars indicate 95% confidence limits for adult males. Sample sizes are indicated next to each symbol. Analysis of variance (Porter 1962) indicates that adult male Chihuahuan pocket mice differ significantly from other classes of the same species and from adult males of *P. merriami*.

During September 1958, adult males of *P. merriami* moved significantly shorter distances between captures on the average than they did during trapping periods in March and July 1958, and May 1959. The mean recapture distance of adult females was significantly greatest in May 1959 and least in September. Young females moved insignificantly greater distances in September than they did in July (Fig. 32).

Adult males and females of this species were not compared because there was an insufficient number of recaptures of adult females. The home range of adult males, however, averaged more than 0.3 ha and that of juveniles nearly 0.2 ha (Fig. 31). The difference between the estimated home range of juveniles and that of adult males was significant at the 0.05 level (Fig. 31). York (1949) found that the average home range of three male pocket mice captured 10 times or more was 0.60 ha, and that of two females was 1.58 ha, which is much larger than was recorded during the present study. In New Mexico, Blair (1943) estimated the average home range of males (*C. eremicus*) as 1.10 ha; of females, 0.44 ha.

Home Range of Nelson's Pocket Mouse.—On the average, adult males moved significantly greater distances between captures than did adult females during March 1958 and May 1959 (Fig. 33). There was not a sufficient number of juveniles captured in March and July 1958 to determine the extent of their movements for these months. During September, however, the mean daily movements of juvenile females were significantly greater than those of adult males and females. During May 1959, adult males moved significantly greater distances than did juvenile females. Dixon (1959) recorded a mean recapture distance for males of 32.6 ±9.8 m during June and July and shorter distances for adult females. For the two aforementioned periods, adult females at Black Gap averaged 22.6 ±4 m.

The mean distances moved by adult males did not differ significantly among any of the trapping periods (Fig. 33). Dixon (1959), on the other hand, found a considerable difference between the mean recapture distance of adult males and adult females recorded from February through May and those recorded for June and July. He also found that females moved less in June and July than they did during the period from February through May. Conversely, I found during this study that females moved significantly greater distances in July than they did in March and May (Fig. 33).

Movements of juvenile females were more extensive during September than for May and December. Differences between the mean recapture distances of juvenile females during September and those for May were highly significant (Fig. 33). The home range of adult males encompassed over 0.30 ha (Fig. 31), whereas adult females ranged over somewhat smaller areas. Although juveniles apparently used less area than did adults, the difference was not significant.

Home Range of the Chihuahuan Pocket Mouse.—The mean daily recapture distances of adult males were

significantly larger than those of adult females for the July and September trapping periods (Fig. 34). Juveniles of both sexes ranged more widely in September than did adult females (Fig. 34).

During July 1958, the ranges of adult males were significantly larger than in any other trapping period (Fig. 34); they were significantly smaller in September than in March and July 1958, but the difference between September 1958 and May 1959 was not significant. The mean daily recapture distances of adult females in September 1958 were significantly less than in March 1958 and May1959, but not July 1958 (Fig. 34).

There were no significant differences in extent of home ranges among adult males, adult females and juveniles (Fig. 31). All of them encompassed approximately 0.25 ha. In southern New Mexico, Blair (1943) estimated the average home range of male *C. eremicus* as 1.10±0.19 ha and that of females as 0.44 ±0.06 ha. The maximum area in hectares for males was 2.24; that of females, 0.58. These represent considerably larger areas than were recorded for *C. eremicus* during the present study (Fig. 31). Conversely, August et al. (1979) reported a mean home range of only 0.047 ha in 11 specimens of *C. eremicus* in Guadalupe Mountains National Park.

Discussion of Home Range and Movements.—According to Blair (1953), within closely related groups, a species living in a sparsely vegetated habitat tends to range more widely than those occurring in an area covered with dense vegetation. The reverse appeared to be true of *C. eremicus* and *C. nelsoni*, however, both in area of the home range and in the mean recapture distance. Nelson's pocket mouse, for example, which was trapped in relatively dense ground cover, ranged significantly (Porter 1962) more widely during July and September 1958 than did the Chihuahuan pocket mouse which was trapped in a sparse ground cover (Figs. 31-33). But this difference may be a function of population density, since the population of *C. nelsoni* was relatively low during those months whereas that of *C. eremicus* was relatively high.

As mentioned previously, my estimates of home ranges of adult *C. eremicus* and *P. merriami* were much smaller than those reported by Blair (1943) for *C. eremicus* in southern New Mexico and by York (1949) for *P. merriami* in western Texas. As observed by Hayne (1950) and Blair (1953), it is difficult to compare the estimates of home range of various investigators, because of the lack of uniformity of treatment among different studies. Many factors may cause a disparity of results, among them (1) distance between trapping sites (Hayne 1950; Stickel 1954); (2) size of plots (Stickel 1960); (3) number of captures used in calculating home range size; (4) density of cover; (5) seasonal density of population (Stickel 1960); (6) breeding condition of the animals (Stickel 1960); and (7) availability of food (Stickel 1960). The first three factors undoubtedly contributed most to the disparity between my estimates and those of Blair (1943) and York (1949).

Extent of range as determined by area presumably occupied by individual mice did not always agree with the results of the mean recapture distance data. For example, judged by mean recapture distances, Merriam's pocket mice moved significantly smaller distances than the other two species. But when home ranges were compared, the home range of *C. eremicus* was significantly smaller (Fig. 31) than that of either of the other two species; that of *P. merriami* was not significantly smaller than that of *C. nelsoni*.

In this study more reliability was placed on mean recapture distance than on a real extent of the home range for the following reasons: (1) There is a much better chance for uniformity of interpretation when ranges are expressed in terms of mean recapture distances. (2) The method involving mean recapture distances requires fewer captures in order to compare the data on the basis of season, age and sex.

Shift in Center of Activity

The center of activity was calculated for each mouse captured during two or more trapping periods. The distance of the shift in center of activity was determined in two ways: (1) The change in center of activity from one period of capture to the next and (2) the change from the first period of capture to each subsequent period. Figure 34 shows the change in center of activity from one period to the next. The changes from the first period of capture are given and analyzed in Porter (1962). The two methods yielded essentially the same results.

The mean shift in the center of activity of each species was comparable to the mean recapture distance of that species for any one period. No one age or sex group of *P. merriami* and *C. nelsoni* showed a significantly greater shift in center of activity than other groups of the same species (Fig. 35). The reason is not understood, but it suggests that the population of *C. eremicus* was not as stable as it was for the other two species. The data were also analyzed to determine whether an interval of one or more trapping periods between periods of capture increased the average shift of the center of activity. This was accomplished by comparing the distance between centers of activity of those animals having an interval of one or more trapping periods between captures with the distance for those having no interval between captures. There was no significant difference between the two (see analysis of variance in Porter 1962).

Miller (1958) observed three typical patterns of movement in his recapture data on *Apodemus*: (1) home range, (2) home range + dispersal, and (3) dispersal. All three patterns were observed in pocket mice during this study, plus movements which might be interpreted as exploratory trips (Plate 17, *P. merriami*, B-17; Plate 18, *C. nelsoni*, B-6, D-8; Plate 19, *C. eremicus*, A-1). Typical home ranges are shown for individuals of each species (Plate 17, *P. merriami*, A-4, B-6, C-13; Plate 18, *C. nelsoni*, A-2, B-5, C-5; Plate 19 *C. eremicus*, A-3, B-6, C-5). For many species of mice dispersal is most frequent as the juveniles approach maturity (Blair 1953). Dispersal was probably more common among juveniles than is indicated by the recapture data, but it was not recorded because individuals leaving the plots were not recaptured.

Several mice displayed movement similar to that Miller (1958) described as dispersal plus home range (Plate 17, *P. merriami*, A-1, A-2, A-18; Plate 18, *C. nelsoni*, A-16, D-9; Plate 19, *C. eremicus*, D-17) except that the extended movements in my examples were between the penultimate and the final captures. Miller's were between the first and second captures and he assumed that the animals remained in their new home ranges. These examples could represent exploratory movements as well as shifts in home range and dispersal because there were no captures at either end of the long dispersal movement. Two or more captures at either end of the long dispersal movements would be needed to determine any shift in home range.

Dispersal

True shifts in home range of a magnitude to be called dispersal rarely were observed during the study, and they occurred only from one trapping period to the next (Plate 17, *P. merriami*, C-13, D-13, E-13; Plate 18, *C. nelsoni*, B-4, C-4, F-4; Plate 19 *C. eremicus*, B-4, C-4, D-4, E-4). Miller (1958) believes that these patterns of apparently aimless wandering represent a continued series of dispersal movements which are best explained as a search by unmated males for breeding females. This seems a plausible explanation for the wanderings of the above mentioned adults during periods of reproduction. The peregrinations of juvenile females possibly may be explained as the movements of a young animal in search of a home range.

Territoriality

Territoriality is the defense of area, usually against others of the same species and sex (Blair 1953). Burt (1943) considers territory as that part of the home range which is defended by fighting or by aggressive gestures against other individuals of the same species. Crowcroft (1955) demonstrated territoriality, as well as a social order, in a population of wild house mice (*Mus musculus*). He found that fighting tended to disperse the population into spatially distinct breeding areas, territorial in function, occupied by one male and one or two females. Conversely, Young et al. (1950) and Scott (1956), who also studied wild-captured populations of this species in the laboratory, found territoriality weekly developed if present at all.

Although direct observation of defense of territory is the best method of demonstrating territoriality, trapping records can give indirect evidence of territorial behavior. For example, if the home ranges of individual animals of one or the other sex or of both sexes are mutually exclusive, territoriality apparently exists.

Although not of general occurrence, several species of small nocturnal rodents are thought to show territorial behavior as determined by occurrence of mutually exclusive home ranges. Because there was

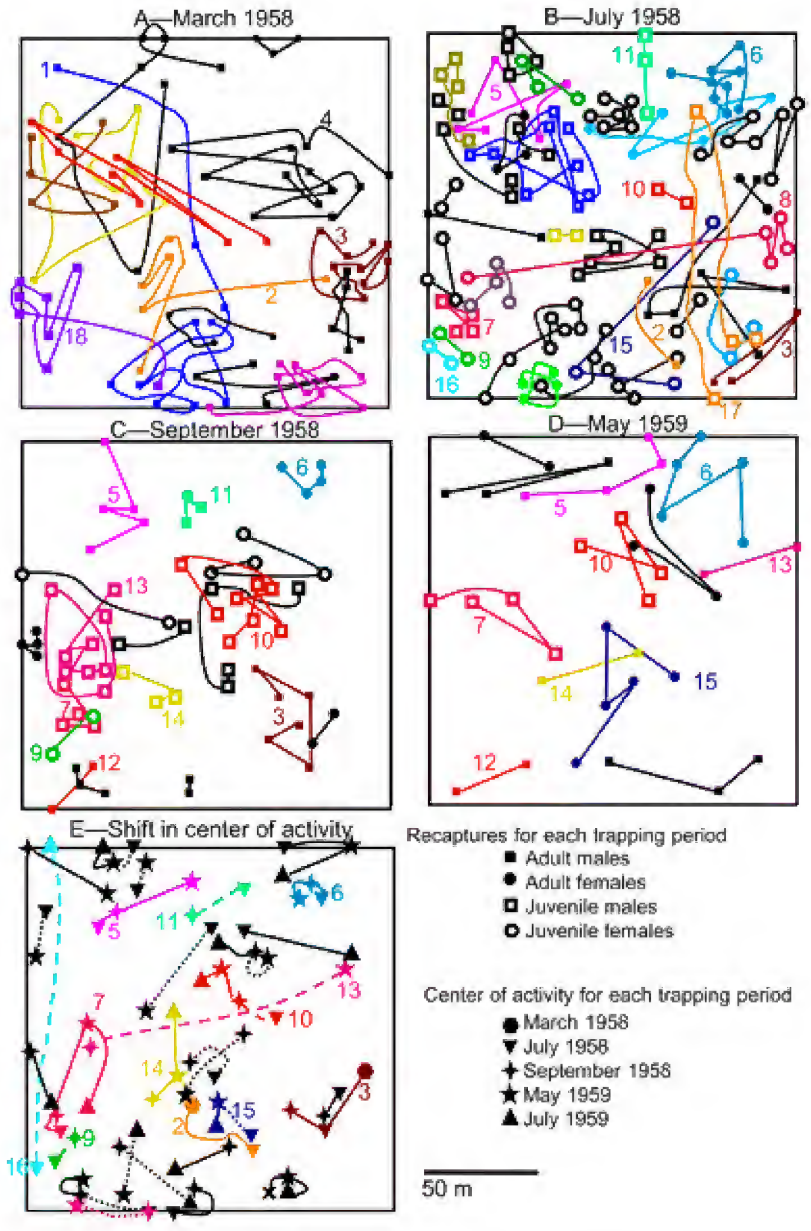

Plate 17. Maps of the seasonal movements, home ranges (A-D), and shifts in home range (E) from one period of capture to the next of *P. merriami* on the Merriami plot, expressed as points of capture. Points of capture or centers of activity for each individual are connected by lines indicating the sequence of capture. Broken lines in part E indicate the change in center of activity between when the animal was a juvenile and when it became an adult. Colors are used when necessary to differentiate individuals with overlapping home ranges or to identify certain animals captured during more than one period. The same color may be used for more than one individual. Numbers identify selected individuals and match the color of the symbols.

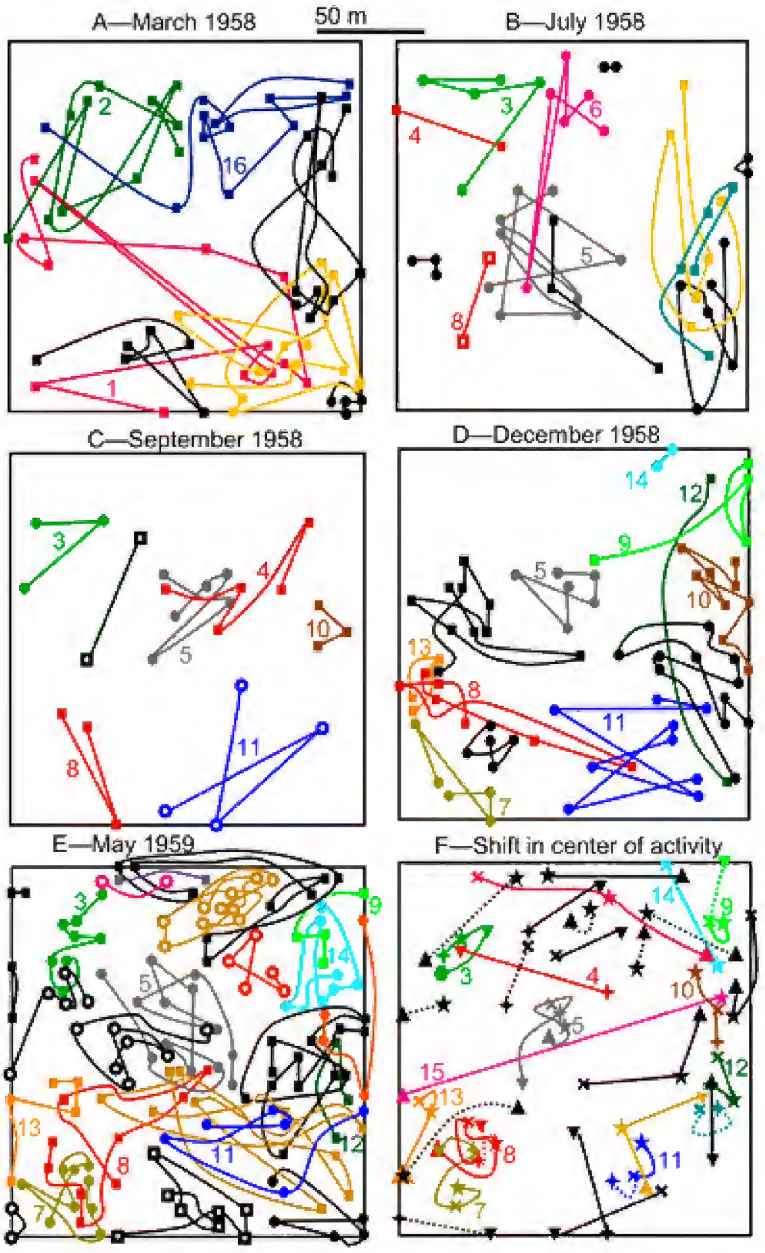

Plate 18. Maps of the seasonal movements, home ranges (A-E), and shifts in home range (F) from one period of capture to the next of *C. nelsoni* on the Nelsoni plot, expressed as points of capture. Points of capture or centers of activity for each individual are connected by lines indicating the sequence of capture. Broken lines in part F indicate the change in center of activity between when the animal was a juvenile and when it became an adult. In parts A-E, males are indicated by squares; females by circles. Closed squares and circles are adults; open squares and circles are juveniles. For the key to shifts in center of activity, see Plate 19. Colors are used when necessary to differentiate individuals with overlapping home ranges or to identify certain animals captured during more than one period. The same color may be used for more than one individual. Numbers identify selected individuals and match the color of the symbols.

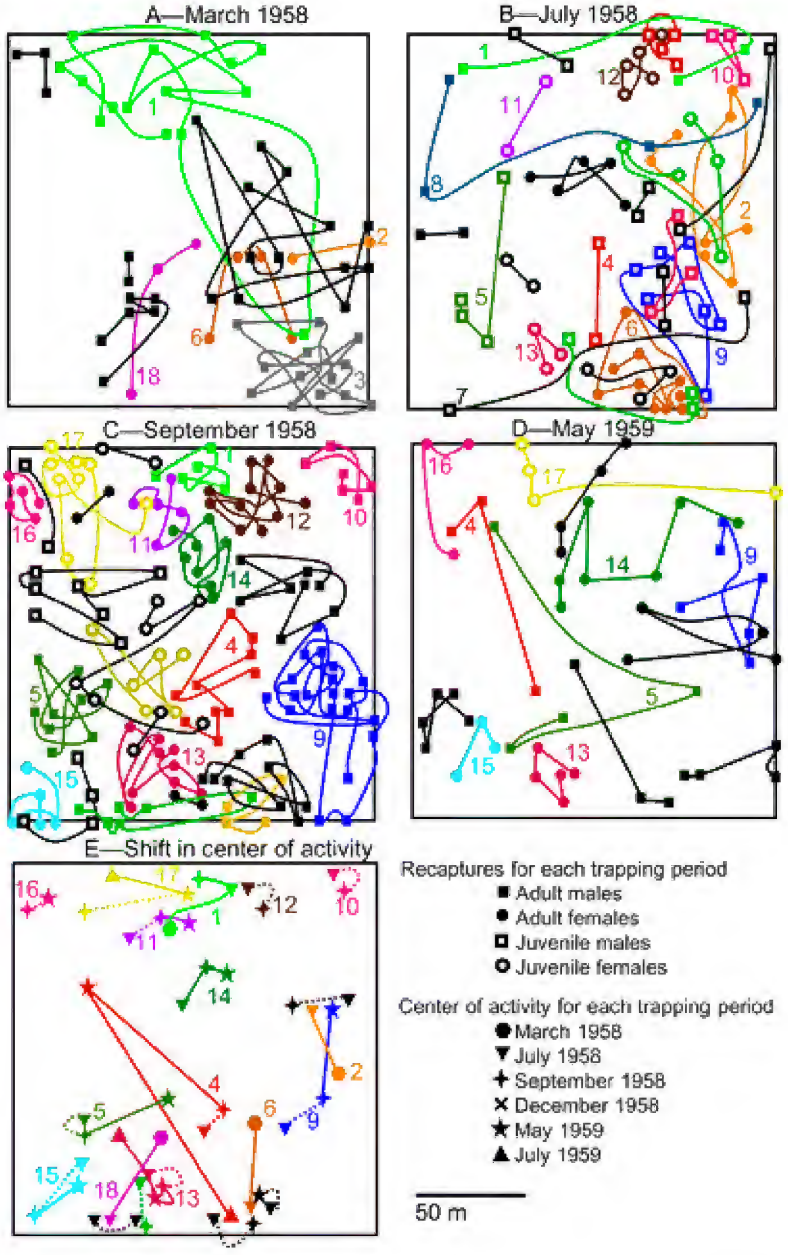

Plate 19. Maps of the seasonal movements, home ranges (A-D), and shifts in home range (E) from one period of capture to the next of *C. eremicus* on the Eremicus plot, expressed as points of capture. Points of capture or centers of activity for each individual are connected by lines indicating the sequence of capture. Broken lines in part E indicate the change in center of activity between when the animal was a juvenile and when it became an adult. Colors are used when necessary to differentiate individuals with overlapping home ranges or to identify certain animals captured during more than one period. The same color may be used for more than one individual. Numbers identify selected individuals and match the color of the symbols.

no broad overlap of ranges among female *Peromyscus leucopus*, Burt (1940) deduced that they possessed territorial behavior. Blair (1951) found similar evidence of territoriality in *Peromyscus polionotus*. Blair (1940) found evidence of territoriality in females of *Microtus pennsylvanicus* based on recapture records. Getz (1961) found that territorial behavior appeared better developed in females than in males and that the size of the defended area of *M. pennsylvanicus* probably was not more than 7 m in diameter.

Blair (1953) pointed out that, although there is considerable antagonism among individuals of the same species of heteromyids, there is little evidence of any defense of territory. He attributed this antagonism to the habit of food storage and the protection of food caches. Blair (1943) observed complementary home ranges in females of *C. eremicus* in April and May, but not in March. Dixon (1959) observed that females of *C. nelsoni* had complementary home ranges from February through July. York (1949) found that the ranges of females of *P. merriami* overlapped during June and July. Data from the present study indicated that adult females of all three species of pocket mice showed a greater tendency toward territoriality than adult males.

Home ranges of adult female Merriam's pocket mice were mutually exclusive during every trapping period except May 1959, at which time there was a slight overlapping. It is possible that the mutually exclusive ranges were a result of the paucity of adult females in the population. The ranges of adult males overlapped somewhat except during periods when the density of the adult population was low (Plate 17). Juvenile females had ranges which were exclusive of those of adult females and other juvenile females. The ranges of juvenile males appeared to be exclusive of those of other juvenile males, but not of adult males.

Ranges of adult female *C. nelsoni* were entirely exclusive of each other during March and September and slightly overlapped during July and December 1958, and May 1959 when the density of the population was high (Plate 18). Ranges of adult males were complementary during periods when population density was low (July and September) with the exception of March. The overlapping observed in March is probably due to the greater movement of adult males as a result of increase breeding activities during that period (Plate 18A). During December and May, when population densities were high, the ranges of adult males overlapped to a greater extent than they did when populations were low. Juvenile females had ranges during May which were generally exclusive of those of adult females and other juveniles (Plate 18D).

Only during July 1958, when there was a low density of adults, were the ranges of adult female *C. eremicus* entirely exclusive of each other (Plate 19B). During the remaining trapping periods, when there were more adults than juveniles, the ranges of adult females overlapped slightly. The seasonal relationship of the ranges of adult males with that of other adult males was similar to that of adult females with other adult females. During July when populations of juvenile *C. eremicus* were at a peak, the ranges of juvenile males were not complementary. The same may be said of juvenile females. During September, however, when there were considerably more adults than juveniles (also more individuals with established home ranges) most of the juvenile males had spatially distinct home ranges, whereas some of the juvenile females did not.

There was a tendency for adult females of all three species of pocket mice to display territorial behavior. This was indicated by the fact that their ranges were spatially distinct when populations were low and nearly distinct when populations were high. Males showed a similar tendency, but to a much lesser extent. During periods of high population density and during the peak of reproduction when males ranged most widely, the ranges of a larger number of adult males overlapped than did those of females. Two factors needing further investigation, which appeared to change the exclusiveness of the ranges of adult males, were (1) reproductive condition of the mice and (2) density of the population. As suggested by Getz (1961), if territoriality were not functioning, one would expect a greater percentage of completely overlapping home ranges during periods of high densities of population than during periods of low densities. The previously mentioned data suggest this to be applicable to the population of adult males. Even the females apparently show some indication of territoriality, since completely overlapping ranges were few.

Territorial tendencies of juvenile female *C. nelsoni* appear to be more pronounced than those of juveniles of the other two species. This is implied by the fact that most young females of Nelson's pocket mouse had ranges which did not overlap even during the periods of greatest density of population (May 1959 trapping period). In addition, juvenile and adult females of Nelson's pocket mouse responded in the population as separate units because the ranges of juveniles overlapped those of adults. The exclusiveness of the ranges of juvenile males and females of the other two species were correlated with the density of the population (Plates 17-19). Thus it appears that territorial behavior functions at an earlier age in Nelson's pocket mouse than it does in the other two species.

Although evidence indicates the presence of territorial behavior in these three species of pocket mice, this hypothesis needs to be tested more extensively with a behavioral study, to determine the extent to which individual ranges are defended.

ACKNOWLEDGMENTS

The Big Bend region was severely overgrazed prior to 1945 when administration of the area was assumed by the National Park Service. In 1955, the Texas State Game and Fish Commission contracted with the Texas Agricultural Experiment Station (Project 965) to study the biological changes taking place in BBNP and the Black Gap Wildlife Management Area. I collected the material upon which this report is based while working on this project. As chair of my doctoral committee, Dr. William B. Davis suggested this problem and supervised my research. I thank him for his many helpful suggestions and advice. Dr. O. Charles Wallmo and Dr. Keith L. Dixon, both of whom conducted research in the Big Bend area on the same ecological project concurrently with this investigation, were particularly helpful with many of the problems and techniques encountered during the course of the field work. The National Park Service staff graciously extended to me and my family facilities of the national park, where we resided during the field work. I am particularly indebted to Mr. George W. Miller, then superintendent of BBNP, for the use of a Park Service vehicle during the study, and also to Mr. Harold J. Broderick, Park Naturalist, for use of the museum preparation room and especially for making the herbarium available.. Mr. Broderick and Mr. Miller issued permits for collecting animals and plants in the Park. My thanks go to Dr. Barton H. Warnock, Sul Ross State College, whose identification of plants proved was an invaluable service. The Bureau of Public Roads provided laboratory facilities and soil sieves. Dr. Robert H. Black, Dean of the College of Agriculture and Home Economics, New Mexico State University provided facilities of the Agronomy Department for the analysis of soil samples. Dr. R. C. Williams of the Department of Agronomy at New Mexico State University deserves particular credit for the use of his laboratory and for giving instruction on techniques of soil analysis. Mr. D. V. Allison and Mr. O. L. Kay, Soil Conservation Service, assisted this work by allowing Mr. August Turner to make two special trips into the study area. The suggestions of Dr. Robert C. Pendleton regarding analysis of the material in this report is much appreciated. The following have been of considerable help: At Texas A&M: Dr. Morris E. Bloodworth and Dr. Harvey Oakes, U. S. Department of Agriculture, helped with early planning of the soil analysis. At the University of Utah: Dr. Charles Wolfe, Department of Genetics, advised me regarding the most practical statistical applications for the data. To my wife Lois G. Porter, I am most grateful for the many hours she spent setting traps, assisting me with the measuring and recording of the vegetation, weighing rock and soil samples, and finally typing the manuscript. Dr. Keith L. Dixon, Utah State University; Dr. Robert C. Pendeleton, Stephen D. Durrant and William H. Behle of the University of Utah, reviewed parts of this manuscript and gave editorial advice. Drs. William B. Davis, Robert A. Darrow, Sewell H. Hopkins, John J. Sperry and O. Charles Wallmo, all members of my advisory committee, critically examined the manuscript.

AFTERWORD

Studies of the mammalian fauna of Texas have a history extending well back into the nineteenth century (Schmidly 2002). The Latin names of two species prominent in this study (Merriam's pocket mouse and Merriam's kangaroo rat) are patronyms honoring C. Hart Merriam, father of the U. S. Bureau of Biological Survey, and founding president of the American Society of Mammalogists. Merriam himself authored the name of *C. nelsoni*, another of the pocket mice examined in this study. Recognizing the importance of the diverse habitats of Texas, Merriam commissioned an extensive biological survey of the state that spanned the years 1889-1906 (Schmidly 2002), and Vernon Bailey was appointed to lead the field work in Texas. The result of this assignment was a classic work (Bailey 1905) on the reptiles and mammals of Texas. Bailey (1905) reported on the range, habitat, behavior, and geographic variation of pocket mice, and described field methods appropriate to each of the species.

Since Bailey, other prominent researchers have taken up the cause of Texas mammalogy. Upon earning his Ph.D. in 1937 under Joseph Grinnell, William B. "Doc" Davis accepted a position at Texas A&M, where he established a notable program in mammalogy (Layne and Hoffmann 1994). Davis authored or coauthored five editions of *The Mammals of Texas*, earning the title of "father of mammalogy" in Texas (Schmidly 2002). Thirteen of Porter's photographs of rodents and carnivores were included in the second edition (Davis 1960), and the third (Davis 1966) and subsequent editions also incorporated information from this study. It was Davis who proposed the study and directed Porter's (1962) graduate committee.

Early mammalogists recognized the Big Bend as an important and fascinating ecosystem. Among his many localities, Bailey (1905) collected a few sites in the Big Bend area, and found both species of *Chaetodipus*. He did not report *P. merriami* from the Big Bend region, though it was collected in other areas of the state. When writing of Merriam's pocket mouse, Bailey's (1905) affection for "the little fellows" is obvious in the warm style characteristic of scientific writing in that period. Though his scientific writing style was more detached, my father often spoke of *P. merriami* in similar terms.

Borell and Bryant (1942) mention a few sporadic mammal collecting trips by other field biologists in the early twentieth century. However, the work of Borell and Bryant (1942) represents the first extensive mammalian study focusing specifically on the Big Bend region, and was done in anticipation of the creation of BBNP. They made five collecting trips, some lasting for several weeks, during 1936-1937, collecting 51 specimens of *C. eremicus*, 29 of *C nelsoni*, and four of *P. merriami*. They incorrectly regarded *P. merriami* as rare in the area, probably because of the use of snap traps, rather than of the hand-collecting method described by Bailey (1905) or of live traps as was done in this study. Borell and Bryant (1942) reported on intraspecific variation and habitat of the specimens they collected. Tasmitt (1954) reported habitat data on pocket mice collected from the Black Gap area (Fig. 2), near the national park.

This study (Porter 1962) filled many gaps noted by Davis (1960) in our knowledge of these species of pocket mice. Subsequent authors of species accounts (Schmidly 1977a, 2004; Best 1994; Best and Skupski 1994) have relied heavily on Porter (1962). The study is unique in focusing intently on pocket mice in the Big Bend area, and in its scope and duration. Few faculty or graduate students have the means or opportunity to live and work full-time in the field for two years. With federal support, Bailey and his field crew worked 2,185 man-days in the field (Schmidly 2002), but spent relatively little time in any one area. Porter's work is particularly noteworthy for addressing nearly every aspect of the natural history of these organisms and their environment. Although previous workers had identified habitat preferences of pocket mice, none had attempted to quantify the habitat and community to the extent done in this study.

In the fifty years since this investigation was completed, there have been few studies comparable. Among the most extensive subsequent studies were Baccus' (1971) dissertation on the effects of vegetation

on small rodents in BBNP and Chapman and Packard's (1974) yearlong survey of the ecology of Merriam's pocket mouse in southern Texas. Baccus (1971) studied vegetational recovery from overgrazing in BBNP and its effects on the distribution of small rodents including pocket mice. Baccus (1971) also reported chiggers collected from mammalian hosts. He extensively sampled a variety of habitats throughout the park during the period 1969-1971. Chapman and Packard's (1974) mark-and-recapture study encompassed 5,922 trap nights and provides important data on abundance, activity, reproduction, movements, home range, and molting that can be compared with the similar data reported by Porter (1962) in this study. Chapman and Packard (1974) also reported on diet and burrow architecture. Their study differs in the habitat and community where the animals were found and thus can be used to evaluate geographic, community, and habitat differences in the species. Ruthven et al. (2003) studied seasonal abundance of *P. merriami* in southern Texas.

Several important studies have been performed in the Big Bend or surrounding regions, but were more broadly focused on mammals or were narrowly focused on one or a few specific questions. Judd (1967) reported on habitat, burrows, and cheek pouch contents of pocket mice in Big Bend. Schmidly (1977b) surveyed the distribution of mammals in the Chihuahuan Desert. Boeer and Schmidly (1977) surveyed mammals along the Rio Grande in BBNP. Wilkins and Schmidly (1979) studied morphology and distribution of pocket mice in the Trans-Pecos of Texas. Franklin D. Yancey, II and his coauthors (Manning et al. 1996; Yancey 1997; Yancey and Jones 2000; Yancey et al. 2006) reported on distribution, habitat, reproduction, molting, and natural history of pocket mice as part of a comprehensive study of mammals in the Big Bend area. Loomis and Crossley (1963), Baccus (1971), Loomis et al. (1972), Loomis and Wrenn (1972, 1973), Whitaker and Easterla (1975), and Wrenn et al. (1976) reported mammalian parasites from BBNP. The results of all of these studies have been cited in the text as appropriate.

Richard Porter's study follows in the tradition of the many natural history investigations (Schmidly 2002) that preceded it. This work added extensively to our knowledge of these species and their ecology and natural history. However, it is to be hoped that future mammalogists, ecologists, and naturalists will continue to expand this work across the dimensions of time, space, and phylogeny.

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APPENDIX I.

Percentage composition of plant species on the population plots based on numbers of individual plants.

	Merriami Plot	Nelsoni Plot	Eremicus Plot
OVERSTORY			
Ephedra	1.0	5.0	0.5
Dasylirion leiophyllum	1.0	13.0	--
Yucca torreyi	3.0	--	--
Acacia constricta	0.5	0.5	5.0
Dalea formosa	--	16.0	--
Prosopis glandulosa	1.0	0.5	6.0
Larrea tridentata	--	6.0	64.0
Guajacum angustifolium	--	1.5	--
Croton dioicus	--	2.0	--
Rhus microphylla	1.0	--	--
Janusia gracilis	--	1.5	--
Ziziphus sp.	--	--	1.0
Fouquieria splendens	--	3.0	5.0
Opuntia leptocaulis	24.0	0.5	9.0
Forestiera	1.0	--	--
Menodora	--	2.0	0.5
Tiquilia greggii	--	10.0	--
Carlowrightia linearifolia	--	3.0	--
Leucophyllum	0.5	16.0	
Ruellia parryi	--	1.0	--
Flourensia cernua	42.0	0.5	1.0
Parthenium incanum	1.0	--	0.5
Porophyllum scoparium	--	2.0	--
Trixis californica	4.0	--	--
Viguiera stenoloba	6.0	3.0	--
Unidentified	12.0	9.0	8.0
UNDERSTORY			
Aristida	2.0	0.5	3.0
Bouteloua breviseta	--	44.0	0.5
Bouteloua eriopoda	1.0	--	--
Bouteloua trifida	--	1.0	--
Dasyochloa pulchella	29.0	5.0	15.0
Agave lechuguilla	20.0	37.0	8.0
Echinocereus stramineus	0.5	0.5	7.0
Mammillaria	0.5	--	--

APPENDIX I. (CONT.)

	Merriami Plot	Nelsoni Plot	Eremicus Plot
Opuntia engelmannii	8.0	0.5	8.0
Opuntia aureispina	1.0	1.0	--
Opuntia schottii	--	2.0	46.0
Senna bauhinioides	--	--	6.0
Krameria	23.0	1.0	--
Jatropha dioica	--	1.0	--
Unidentified	1.0	0.5	5.0

APPENDIX II.

Characteristics of the important species of plant cover on the population plots. Relative dominance is calculated according to Cottam and Curtis (1956).

	Mean Area at Base (cm^2)			Relative Dominance			Mean Height (cm)		
	Merriami Plot	Nelsoni Plot	Eremicus Plot	Merriami Plot	Nelsoni Plot	Eremicus Plot	Merriami Plot	Nelsoni Plot	Eremicus Plot
OVERSTORY									
Ephedra	1,030	1,250	432	1.5	5.1	0.13	78.0	59.9	38.1
Dasylirion leiophyllum	6,584	6,600	--	6.4	70.3	--	85.1	140.7	--
Yucca torreyi	16,437	--	--	48.0	--	--	151.1	--	--
Dalea formosa	--	130	--	--	1.8	--	--	45.7	--
Prosopis glandulosa	399	245	20,221	0.4	0.1	56.7	99.1	12.7	95.3
Larrea tridentata	--	487	759	--	2.4	26.3	--	74.4	81.0
Fouquieria splendens	--	369	395	--	0.9	0.9	--	208.8	189.5
Tiquilia greggii	--	125	--	--	1.0	--	--	37.8	--
Leucophyllum	1,139	841	--	0.6	10.7	--	129.5	72.4	--
Flourensia cernua	475	46	308	18.8	0.02	0.2	57.4	63.5	92.7
Parthenium incanum	39	--	248	0.06	--	0.07	40.6	--	83.8
Trixis californica	290	--	--	0.8	--	--	42.7	--	46.7
Opuntia leptocaulis	790	248	84	17.9	0.1	0.4	41.4	61.0	--
UNDERSTORY									
Bouteloua eriopoda	46	--	--	0.01	--	--	10.2	--	--
Bouteloua breviseta	--	357	87	--	7.9	0.02	--	50.5	25.4
Dasyochloa pulchella	36	91	190	0.19	0.2	1.6	3.8	6.1	8.1
Agave lechuguilla	2,333	4,594	359	12.6	82.5	1.5	26.2	32.0	31.5
Krameria	2,257	2,071	--	9.7	1.0	--	23.6	26.7	--
Jatropha dioica	--	79	--	--	0.1	--	--	43.2	--
Opuntia engelmannii	43,568	7,297	11,013	73.0	1.8	53.1	50.5	35.6	25.7
Opuntia schottii	--	1,700	1,300	--	2.1	31.7	0.0	11.2	10.7

APPENDIX III.

Average percentage composition of vegetation in habitat types (average percentage of total samples taken in each habitat type).

	Rock-free Flats	Sandy Washes	Fine Gravelly Plains	Fine Gravelly Foothills	Fine Gravelly Hillsides	Coarse Gravelly Foothills	Coarse Stony Sandy Hillsides	Coarse Stony Mountainsides	Rough-broken Mountainsides
OVERSTORY SPECIES									
Ephedra	< 0.5	0	0	< 0.5	0	3	8	1	5
Dasylirion leiophyllum	0	0	0	6	3	5	0	7	3
Yucca elata	0	3	0	0	0	0	0	0	0
Yucca torreyi	0	0	0	2	0	2	0	0	0
Celtis laevigata	0	0	0	0	0	2	0	0	0
Atriplex canescens	3	0	0	3	0	0	0	0	0
Iresine leptoclada	0	0	0	0	0	0	0	0	1
Selinocarpus angustifolius	0	0	0	0	0	0	17	1	1
Berberis trifoliolata	0	0	0	0	0	0	0	0	2
Acacia constricta	1	0	0	3	1	0	4	1	0
Acacia mimata	0	14	0	0	0	0	0	0	0
Acacia greggii	2	5	< 0.5	1	1	1	1	2	1
Acacia angustissima var. texensis	0	0	0	0	5	0	0	1	0
Calliandra eriophylla	0	0	0	0	2	0	0	0	0
Dalea formosa	0	0	0	< 0.5	7	0	0	2	0
Krameria	0	0	1	5	0	3	1	2	2
Mimosa dysocarpa	0	0	0	0	1	0	0	1	1
Prosopis glandulosa	19	0	< 0.5	4	15	0	0	1	0
Larrea tridentata	63	13	49	0	22	0	35	1	0
Porlieria angustifolia	0	0	5	0	0	3	0	1	2
Koeberlinia spinosa	0	0	< 0.5	0	0	1	0	0	0
Janusia gracilis	0	0	0	0	0	0	0	1	3
Bernardia obovata	0	0	0	0	0	0	0	0	2
Croton dioicus	0	0	0	< 0.5	0	0	0	1	1
Jatropha dioica	< 0.5	0	22	0	0	12	0	34	5
Rhus microphylla	0	0	0	0	0	< 0.5	0	0	0

APPENDIX III. (CONT.)

	Rock-free Flats	Sandy Washes	Fine Gravelly Plains	Fine Gravelly Foothills	Fine Gravelly Hillsides	Coarse Gravelly Foothills	Coarse Stony Sandy Hillsides	Coarse Stony Mountainsides	Rough-broken Mountainsides
Schaefferia cuneifolia	0	0	0	0	0	0	0	0	1
Condalia	0	0	0	0	1	0	0	1	0
Condalia lycioides	< 0.5	0	0	1	0	< 0.5	0	0	0
Condalia obovata	2	0	0	0	0	0	0	0	0
Hibiscus coulteri	0	0	0	1	2	< 0.5	0	0	1
Hibiscus denudatus	0	0	0	0	0	0	0	0	1
Ayenia microphylla	0	0	0	0	0	5	0	0	0
Fouquieria splendens	< 0.5	0	2	0	1	0	10	3	0
Opuntia engelmannii	2	2	2	6	3	5	3	3	7
Opuntia imbricata	0	0	0	< 0.5	0	< 0.5	0	0	0
Opuntia leptocaulis	3	9	0	3	3	3	12	0	7
Opuntia macrocentra	0	5	3	4	5	8	2	4	2
Opuntia rufida	0	0	3	0	0	0	0	3	0
Foresteria	0	0	0	0	0	1	0	0	0
Menodora	0	0	0	0	0	< 0.5	2	0	1
Tiquilia greggii	0	0	0	0	0	0	1	3	0
Aloysia	0	0	0	0	0	0	0	0	2
Aloysia wrightii	0	0	0	0	1	0	0	1	0
Lycium	< 0.5	0	0	1	0	< 0.5	0	0	0
Lycium berlanderi	0	0	0	< 0.5	0	0	0	0	0
Leucophyllum	0	0	0	0	0	1	0	7	3
Carlowrightia linearifolia	0	0	0	0	0	9	0	0	9
Ruellia parryi	0	0	0	0	0	0	0	8	17
Flourensia cernua	2	0	0	21	0	< 0.5	0	0	0
Gutierrezia	2	0	0	5	9	2	0	0	2
Parthenium incanum	< 0.5	0	3	12	0	11	0	0	1
Porophyllum scoparium	0	39	0	0	0	3	0	1	0
Gymnosperma glutinosum	0	0	0	6	10	9	0	0	4
Trixis californica	0	0	0	< 0.5	0	2	0	1	0
Viguiera stenoloba	< 0.5	2	4	7	5	3	1	3	5
Jefea brevifolia	0	0	0	0	1	0	0	0	4

APPENDIX III. (CONT.)

	Rock-free Flats	Sandy Washes	Fine Gravelly Plains	Fine Gravelly Foothills	Fine Gravelly Hillsides	Coarse Gravelly Foothills	Coarse Stony Sandy Hillsides	Coarse Stony Mountainsides	Rough-broken Mountainsides
UNDERSTORY SPECIES									
Selaginella lepidophylla	0	0	0	0	0	0	0	0	2
Aristida	5	0	0	5	3	3	6	1	1
Aristida adscensionis	0	0	0	0	0	0	0	3	0
Bouteloua breviseta	0	0	8	2	6	13	42	54	28
Bouteloua curtipendula	0	0	0	1	3	5	0	0	3
Bouteloua eriopoda	0	0	0	6	3	4	0	0	1
Bouteloua trifida	1	0	0	2	6	15	0	0	0
Cathestecum erectum	0	0	0	1	23	0	25	3	7
Heteropogon contortus	0	0	0	0	0	5	0	0	2
Pleuraphis mutica	1	0	0	0	3	0	6	0	2
Leptochloa dubia	0	0	0	0	0	1	0	0	0
Muhlenbergia porteri	0	0	0	< 0.5	1	3	0	0	4
Panicum	0	0	0	0	3	0	0	0	0
Panicum hallii	0	0	0	0	0	0	0	0	2
Setaria	0	0	0	4	0	13	0	0	1
Sporobolus	28	0	0	0	0	0	2	0	0
Sporobolus cryptandrus	0	44	0	0	0	0	0	0	0
Sporobolus wrightii	0	0	0	0	10	0	0	0	0
Digitaria californica	0	0	0	0	0	2	0	0	12
Dasyochloa pulchella	8	13	0	56	1	13	3	1	0
Tridens muticus	1	0	0	< 0.5	2	9	0	0	5
Cyperus	0	0	0	0	0	1	0	0	0
Agave lechuguilla	5	0	85	18	20	7	0	35	19
Dondia suffrutescens	26	0	0	0	0	0	0	0	0
Euphorbia antisyphilitica	0	0	0	0	0	0	0	0	4
Echinocereus	4	0	2	0	0	0	0	0	0
Echinocereus stramineus	1	0	5	< 0.5	3	0	3	1	1
Opuntia schottii	17	0	0	0	0	0	6	0	1
Heliotropium confertifolium	0	0	0	0	0	0	1	0	0